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Environmental Constraints on the Distribution of the Non-native Grass, *Microstegium vimineum*

Patrice G. Cole

University of Tennessee - Knoxville

To the Graduate Council:

I am submitting herewith a dissertation written by Patrice G. Cole entitled "Environmental Constraints on the Distribution of the Non-native Grass, *Microstegium vimineum*." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

Jake F. Weltzin, Major Professor

We have read this dissertation and recommend its acceptance:

Dan Simberloff, Joanne Logan, Jim Drake, Michael Huston

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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Environmental Constraints on the Distribution of the Non-native Invasive Grass, *Microstegium vimineum*

A dissertation presented for the Doctor of Philosophy Degree

The University of Tennessee, Knoxville

Patrice G. Cole

May 2003

DEDICATION

I dedicate this dissertation to my mother, Rosavilla Grinnell Cole, who instilled in me a love of learning and who worked hard and sacrificed much so that I could achieve my educational goals. I will forever be grateful for her encouragement and support.

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I would not have completed this dissertation without the guidance and support of my advisor, Jake Weltzin, and I am very grateful for the many hours he spent working with me, from hammering out ideas at the white board to shoveling soil in the field. Committee member Michael Huston was instrumental in the development of the research framework, and he provided financial support through EPA Star Grant R825157-01-0. I thank committee members Dan Simberloff, Joanne Logan, and Jim Drake for their time and intellectual contributions. Mike Newman with the University of Tennessee Statistical Consulting Center provided essential statistical support, and I am very grateful for his patience and wit. I was assisted in the field and greenhouse by Caroline Devan, Patrick Kerr, Joshua Kerr, Phillip Allen, Travis Belote, Doug Berry, and Sara Drake. Patricia Parr arranged for access to my field research sites in the Oak Ridge National Environmental Research Park. Chris Fleming and Larry Pounds provided assistance in plant taxonomy. The University of Tennessee Department of Ecology and Evolutionary Biology provided partial funding for this research.

ABSTRACT

Microstegium vimineum (Trin.) A. Camus, commonly known as Japanese grass, is a non-native plant of particular ecological concern in the United States due to its potential impact on native ecosystems, yet surprisingly little is known of its ecological requirements. In spite of its rapid expansion throughout its North American range, *M. vimineum* tends to occur in discrete patches on the landscape and is frequently found in disturbed understory habitats along roadbanks, floodplains, and nearby mesic forest. It is not found in many apparently suitable locations, which suggests that certain environmental factors, or interactions of factors, limit the distribution of this invasive grass. I used a combination of field and greenhouse experiments and a biogeographical survey to examine environmental factors that might cause the complex pattern of presence/absence and performance exhibited by this species.

The biogeographical survey was designed to (1) identify environmental factors that limit the distribution of this species to certain positions on the landscape (i.e., explain presence/absence), and (2) quantify the performance (i.e., height and biomass) of this species in response to environmental gradients. Within the study area, *M. vimineum* exhibited the broad environmental tolerance of many "weedy" species. Soil pH was the only environmental variable, among those measured, that was correlated with the presence of *M. vimineum*, whereas canopy openness and other species biomass are the most important variables that explain the performance of *M. vimineum*. This information can be used to predict habitats that are vulnerable to invasion by this species, prioritize

the species as a land management concern, and guide the development of effective control strategies.

Light and water are important resources for all plants, and it has been suggested that these resources are mutually substitutable, at least within a certain range of resource levels. I conducted a greenhouse experiment to test a hypothesized light/water trade-off in *M. vimineum*, whereby light and water would be mutually substitutable and would have an interactive effect on plant growth. The experiment consisted of a randomized, 4 x 5 factorial design that included light levels (75%, 25%, 10%, 5%, and 2% sunlight) and soil moisture levels (40%, 30%, 20%, and 10%) that encompassed the ranges likely to be experienced by this species in a natural setting. Results demonstrate a light/water trade-off in *M. vimineum* in terms of root, shoot, and total biomass accumulation (light × water interaction, $p<0.0001$). Light and water are mutually substitutable resources in this species, because plants grown in low light attained greater biomass when provided with more water, and plants grown in drier soils attained greater biomass when provided with more light ($p<0.005$). However, light is a better substitute for water than water is a substitute for light ($p=0.005$). Shifts in biomass accumulation between roots and shoots does not appear to be the mechanism responsible for the trade-off ($p>0.05$), but stomatal conductance remains a plausible mechanism that should be tested in future research.

Within its introduced range, *M. vimineum* often occurs as extensive, dense patches with sharp boundaries and distinct gaps in cover. One example of this distributional pattern was observed relative to the native shrub *Asimina triloba* (pawpaw), whereby dense *M. vimineum* cover ended abruptly at the drip line of the *A. triloba* patch and was absent beneath the *A. triloba* canopy. I conducted field and greenhouse experiments to

test several hypotheses regarding the causes of this observed pattern of *M. vimineum* distribution, including allelopathy, lack of seed dispersal, soil moisture limitations, and light limitations. I concluded that light reduction by the *A. triloba* canopy prevented establishment of *M. vimineum* beneath this shrub. In a complementary field shade experiment, a 60% reduction in ambient understory light reduced seedling survival, and the threshold for seedling survival is between 60% and 16% ambient understory light. These findings suggest that habitats in deep shade are less vulnerable to invasion by this non-native grass.

This research is the first explicit investigation of environmental constraints on the distribution of *M. vimineum*. I suggest that the complex pattern of this species' distribution and abundance in its introduced range is the result of interactions between resources, especially light and water, and seed dispersal limitations. The importance of maintaining undisturbed native vegetation is one of the conservation implications of these findings. My survey results are consistent with other reports that roads and trails are the most common habitat in which *M. vimineum* is found in its introduced range, and these linear gaps in forested systems appear to provide a corridor for the spread of this non-native species. Forest fragmentations by development, including agriculture, increases the amount of edge habitat that favors the establishment of *M. vimineum* and increases the opportunities for its invasion into nearby intact forest. Comparative studies of this species in its native and introduced ranges and research on its ecological impacts are needed.

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CHAPTER 1

INTRODUCTION

Background

Many ecologists consider the invasion of non-native species into natural ecosystems to be one of the greatest threats to global biological diversity, second only to habitat alteration (Elton 1958, Cronk and Fuller 1995, Williamson 1996, Luken and Thieret 1997, Dukes and Mooney 1999). Non-native species often attain high levels of abundance because they have escaped diseases, predators, parasites, or limiting climatic factors in their new environment. Likewise, native species often lack the defenses or competitive ability that would allow co-existence with non-native species. As a result, non-natives sometimes displace natives, reducing community species richness, changing ecosystem functions (Vitousek and Walker 1989), and altering the "sense of place" that is promoted by native species assemblages (Williamson 1996).

Considerable research has been devoted to determining life history characteristics that predict which species are likely to be successful invaders and displace native species. Baker (1965) developed a list of 20 characters for defining "the ideal weed." Noble (1989) attempted to refine and expand the identification of the attributes of successful terrestrial plant invaders. Ehrlich (1989) looked for patterns among successful vertebrate invaders that might be used to characterize the "typical" animal invader and invasion process. Rejmanek and Richardson (1996)

reported that invasiveness of pines and, perhaps, other woody species is predictable on the basis of a few biological characteristics. Similarly, Reichard and Hamilton (1997) used a retrospective analysis of several attributes of woody plants introduced to North America to develop a list of traits that could be used to predict which species would become invasive.

Likewise, much effort has been expended on the search for generalizations about the characteristics that make certain habitats more vulnerable to invasion. For example, Elton (1958) first hypothesized that habitats of low species richness were likely to be more invasible than areas of high species richness, because there are more available niches in low-richness habitats. It has been proposed that habitats of high species richness are less invasible, because resident species sequester a broad range of resources (MacArthur and Wilson 1967, McNaughton 1983, Pimm 1991, Tilman 1997). More recent research has suggested that areas of high species richness might actually be more easily invaded, due to the high availability of resources that promotes high native species richness (Stohlgren et al. 1999).

However, as noted by Williamson (1996), attempts to develop predictors of successful invaders or especially invasible habitats have been largely unsuccessful. It appears that the success of an invasion, as well as the subsequent effect on the invaded ecosystem, is the result of the particular interaction between the life history traits of a species and the biotic and abiotic characteristics of potential new habitat. Stohlgren et al. (1999) suggested that integrated studies of a particular species in a particular habitat would be more valuable than searching for generalizations about the traits of successful invaders or invasible habitats. I used this approach to examine the

interaction of environmental factors that constrain the distribution of *M. vimineum* to certain landscape positions in a portion of its introduced range in the southeastern United States.

Microstegium vimineum

Microstegium vimineum (Trin.) A. Camus (common names include Japanese grass, Vietnamese stilt grass, Nepalese browntop, and Chinese packing grass) is a C_4 annual grass of Asiatic origin, ranging from India to Japan. First collected in the Western Hemisphere in 1919 in Knoxville, Tennessee (Fairbrothers and Gray 1972), it is currently established throughout the eastern United States (Redman 1995). Its rapid expansion of range since its introduction, and its tendency to become the dominant understory plant species in many invaded habitats, has raised concerns about its potential to displace native plant species. For example, it is one of the 35 non-native plant species that have been identified as serious threats to the natural ecosystems of the Great Smoky Mountains National Park. In fact, it is ranked highest in significance of impact in the Smokies (National Park Service 1999). It is also ranked lowest in feasibility of control, because so little is known of its autecology or synecology.

Autecology

M. vimineum is a C_4 (warm-season) grass that has been shown to grow under light conditions that range from 100% to 5% sunlight, and its photosynthetic response has been reported to saturate at 25% sunlight (Winter et al. 1982). Morphological and biochemical plasticity has been observed in *M. vimineum* plants grown in a range of

light levels (Winter et al. 1982). *M. vimineum* tolerates the low light typical of understory habitats yet maintains characteristics of plants adapted to high light environments, such as rapid induction loss and rapid stomatal movements in variable light (Horton and Neufeld 1998).

Synecology

Although many observers have recognized the potential impact of this plant on native ecosystems (Cusick 1986, Redman 1995, Mehrhoff 2000), surprisingly little is known of its ecological requirements and actual impacts. *M. vimineum* is slow to invade undisturbed vegetation but rapidly fills disturbed, mesic, shaded areas, where it often forms dense monocultures (Barden 1987). Kourtev et al. (1999) reported that non-native earthworm densities and soil pH, available nitrate, and net potential nitrification were significantly higher in soils under *M. vimineum* compared to native vegetation in hardwood forests of New Jersey; however, it cannot be concluded from their data that *M. vimineum* caused the observed changes in soil properties or even earthworm densities.

M. vimineum is frequently found in disturbed understory habitats along roadbanks, streambanks, floodplains, and nearby mesic forest. Most of the sites in Maryland where *M. vimineum* was established were acidic (pH 5.8 to 4.8), high in nitrogen, and had soil textures that ranged from moist, well-drained silty loams to loamy sands (Redman 1995). At the majority of sites, *M. vimineum* occurred on bare soils not occupied by other species, or occupied by sparse grasses and herbs. However, it is unknown whether these low diversity conditions reflect those prior to invasion by *M. vimineum* or those that resulted from the invasion *per se*. Some

information sources state that *M. vimineum* can replace competing ground vegetation/native plants within 3 to 5 years, but actual data to support such claims are lacking.

There is no information on the particular mechanisms by which *M. vimineum* invades and potentially dominates native plant communities. Anecdotal evidence and the pattern of this species' distribution on the landscape suggest that its seeds are naturally dispersed by overland flow of stormwater and may be introduced by humans as an unintentional constituent of topsoil or mulch (Mehrhoff 2000). It is possible that animals also disperse the seeds by eating and defecating them. Wild turkeys have been observed eating *M. vimineum* seeds (Cole, personal observation).

Once established, *M. vimineum* is said to be capable of persisting by virtue of a seed bank that can quickly germinate and replace plants removed by some type of disturbance (Barden 1987). In spite of its rapid expansion throughout its North American range, *M. vimineum* tends to occur in discrete patches on the landscape. Redman (1995) noted that, in Maryland, *M. vimineum* was not found in many apparently suitable locations. This suggests that certain environmental factors, or interaction of factors, limit the distribution of this invasive grass.

I conducted field surveys and field and greenhouse experiments to (1) develop fundamental information on the distribution and habitat characteristics of *M. vimineum* on a landscape in the southeastern United States, (2) determine the environmental factor(s) that constrain its distribution on that landscape, and (3) use this species to test a light/water trade-off that has been hypothesized for plants in general. Chapter 2 describes a biogeographical survey of *M. vimineum* in the Oak

Ridge National Environmental Research Park, Oak Ridge, Tennessee. A greenhouse experiment to test the light/water trade-off hypothesis is presented in Chapter 3. Chapter 4 describes a series of field and greenhouse experiments to test hypotheses regarding the environmental factors that cause a particular pattern of *M. vimineum* distribution relative to a native, woody plant (*Asimina triloba*, pawpaw). In Chapter 5, I synthesize the results of these investigations and offer suggestions on future research.

CHAPTER 2

ENVIRONMENTAL CORRELATES OF THE DISTRIBUTION AND ABUNDANCE OF *MICROSTEGIUM VIMINEUM*, IN EAST TENNESSEE, USA

Introduction

Microstegium vimineum (Trin.) A. Camus, commonly known as Japanese grass, is a non-native plant of particular ecological concern in the United States (Cusick 1986, Redman 1995, Mehrhoff 2000). Its rapid expansion of range since its introduction in the early 1900s, and its tendency to become the dominant understory plant species in many invaded habitats, have raised concerns about its potential to displace native plant species (Cusick 1986, Redman 1995). Although many observers have recognized the potential impact of this plant on native ecosystems (Cusick 1986, Redman 1995, Kourtev et al. 1999, Mehrhoff 2000), surprisingly little is known of its ecological requirements.

Microstegium vimineum is a C_4 annual grass of Asiatic origin. Its native range includes India, Pakistan, Nepal, China, Korea, and Japan (Tu 2000). First collected in the Western Hemisphere in 1919 in Knoxville, Tennessee (Fairbrothers and Gray 1972), it is currently established throughout the eastern United States (Redman 1995). *M. vimineum* is frequently found in disturbed understory habitats along roadbanks, streambanks, floodplains, and nearby mesic forest. Although it is slow to invade undisturbed vegetation, it can rapidly spread across disturbed, mesic,

shaded areas, where it can form dense monocultures (Barden 1987). Most of the sites in Maryland where *M. vimineum* was established were acidic (pH 5.8 to 4.8), high in nitrogen, and had soil textures that ranged from moist, well-drained silty loams to loamy sands (Redman 1995). At the majority of sites, *M. vimineum* occurred on bare soils not occupied by other species, or soils occupied by sparse grasses and herbs.

In spite of its rapid expansion throughout its North American range, *M. vimineum* tends to occur in discrete patches on the landscape. Redman (1995) noted that, in Maryland, *M. vimineum* was not found in many apparently suitable locations. This fact suggests that certain environmental factors, or interactions of factors, limit the distribution of this invasive grass. Soil moisture (Williams 1998), soil texture (Hunt and Zaremba 1992, Redman 1995), disturbance (Barden 1987), and dispersal (Mehrhoff 2000) have been suggested as factors that limit this species' distribution.

Although Barden (1987) offered anecdotal information regarding the types of habitats the species had invaded in North Carolina, and Redman (1995) provided a qualitative description of invaded habitats in Maryland, neither study systematically and quantitatively analyzed the relationship between habitat characteristics and *M. vimineum* growth response. This information would be valuable for predicting the habitats that are vulnerable to invasion by this species, prioritizing the species as a land management concern, and guiding the development of effective control strategies.

I conducted a landscape-level survey of the distribution of this species, and collected data on biotic and abiotic variables posited to explain the observed patterns of distribution, in the Oak Ridge National Environmental Research Park, Oak Ridge,

Tennessee, in summer 2000. The goals of this study were to (1) identify environmental factors that limit the distribution of this species to certain positions on the landscape (i.e., explain presence/absence), and (2) quantify the performance (i.e., height and biomass) of this species in response to environmental gradients. My specific objectives were to (1) identify locations that supported *M. vimineum* as a patch >1 m^2; (2) quantify *M. vimineum* height, density, and biomass at each location; (3) describe the characteristics of *M. vimineum* habitats in terms of canopy openness, soil characteristics, plant community type, and land use history; and (4) for a subset of representative sites, construct predictive models of *M. vimineum* growth response based on environmental factors.

Methods

Site Description

I conducted the survey at the Oak Ridge National Environmental Research Park (hereafter the Research Park), which consists of 5008 ha of eastern deciduous forest, upland mixed forest, streams, and reservoirs within the Department of Energy reservation at Oak Ridge in eastern Tennessee (Anderson and Roane Counties), USA. The climate of the Research Park is relatively mild, with an average winter temperature of 6°C and an average summer temperature of 24°C; mean annual precipitation is about 1500 mm (National Weather Service 2002).

The Research Park is located in the Ridge and Valley Physiographic Province (Atwood 1940) and is characterized by a series of narrow, elongated ridges and slightly broader intervening valleys that trend northeast to southwest. Elevation

ranges from 250 m to 420 m above mean sea level, with topographic relief from ridge crests to valley floors averaging 100 m. Bedrock is dominated by calcareous siltstones and limestones, including the Conasauga and Chickamauga Groups (Oak Ridge National Laboratory 2000). The long history of human land use in the region (Federal Writers' Project 1939) has created many opportunities for non-native plants to be introduced intentionally or accidentally. To date, 167 non-native or "exotic" species have been identified in the Research Park (ORNERP 2001), part of the more than 1,100 species of vascular plants in that landscape (ORNL 2000). *M. vimineum* is widely distributed throughout the Research Park and is a dominant understory plant species in some areas of the park (Pounds et al. 1993, Drake et al. 2001).

Landscape Level Distribution of *M. vimineum*

Between June 1 and October 31, 2000, I recorded all locations in the Research Park where *M. vimineum* occurred as a patch >1 m^2. This species is common along the sides of roads and trails, so I traveled all of the accessible roads in the Research Park and noted its presence. At each location where *M. vimineum* extended from the roadside into adjacent habitat, I estimated the size of the patch and examined the surrounding area for additional patches farther from the roadside. I also subjectively searched wooded areas beyond the roadside where I expected to find suitable habitat for this species (e.g., floodplains, wetlands). In addition, I conducted a thorough search for this species in the 100 ha Walker Branch watershed research area (Trettin et al. 1999).

In September, at the time of peak standing biomass for this species, I estimated the maximum height, density, and aboveground biomass of *M. vimineum* in

each previously located patch. I used a 0.25 m^2 round quadrat to delineate one sample plot arbitrarily located as representative of the *M. vimineum* stand in each patch, measured the height of the tallest shoot within the plot, and clipped all *M. vimineum* shoots within the plot at ground level. Shoots were oven dried at 50°C to constant mass. I also noted other plant species that were present at the time.

Detailed Site Characterizations

Three ~5 ha sites were chosen for more intensive sampling and characterization to determine environmental gradients that constrained *M. vimineum* to the particular locations it occupied at each site. These sites included (1) a wooded area southwest of the intersection of U.S. Hwy. 95 and Jones Island Road (JIR), (2) a recently disturbed area west of the intersection of U.S. Hwy. 95 and Bethel Valley Road (BVR), and (3) an old home site in the Walker Branch watershed (WBW). JIR was chosen as a representative example of invaded understory habitat in the Research Park. I chose WBW because the presence of this species in the Walker Branch environmental research area was of particular concern to land managers in charge of that area (Michael Huston, personal communication). I chose BVR because it was the only open-canopy site in the Research Park that supported a tall, dense patch of *M. vimineum.* The *M. vimineum* cover at each of these three locations exhibited very distinct boundaries and gaps that suggested the presence of one or more strong environmental gradients that constrained its distribution to certain portions of the site.

JIR had an open understory with tall, dense *M. vimineum* cover. Remnants of a building and buried household refuse on one corner of the site suggest that it was a homestead prior to the formation of the Oak Ridge Reservation, although specific

land-use history data for this and most other sites in the Research Park were unavailable. The site is nearly flat, with a slight slope to the east. The plant community on the site was typical of second-growth mixed mesophytic forest (Barbour and Billings 1998). Dominant tree species included *Acer negundo* L., *Acer saccharum* Marsh., *Pinus taeda* L., *Fagus gradifolia* Ehrh., *Juniperus virginiana* L., *Platanus occidentalis* L., and *Nyssa sylvatica* Marsh. Understory species included scattered individuals of *Vitis rotundifolia* Michx., *Rhamnus caroliniana* Walt., *Elymus virginicus* L., *Verbesina virginica* L., *Euonymous americanus* L., and *Rhus toxicodendron* L. The site is bordered by a two-lane highway, an unpaved road, and a pine plantation that had been clearcut within the past 5 years.

BVR is bordered by a two-lane highway and an unpaved road. Most of the site was clearcut in 1999 and still showed signs of soil disturbance by heavy equipment. Topsoil was virtually absent from much of the site, and chert fragments and woody debris littered the soil surface in many places. The site was nearly flat. Dominant tree species on the uncut portion of the site included *Carpinus caroliniana* Walt., *Diospyros virginiana* L., *Sassafras albidum* (Nutt.) Nees, *Liriodendron tulipifera* L., *Liquidambar styraciflua* L., and *Ulmus alata* Michx. Understory species included *Ambrosia artimisiifolia* L., *Lespedeza stipulacea* Maxim., *Desmodium paniculatum* L., *Asplenium platyneuron*, *Lonicera japonica*, and *Lobelia syphalytica* L. A tall, dense patch of *M. vimineum* extended from the unpaved road, across the clearcut portion of the site, and for several meters into an intact remnant of pine plantation.

WBW is at the site of an old homestead in the interior of Walker Branch Watershed Research Area. This relatively level, open understory site was bordered by a small, ephemeral stream and steep to moderately steep slopes. Dominant tree species included *Juglans nigra* L., *Cercis canadensis* L., *Morus rubra* L., *Cornus florida* L., *Acer negundo*, and *Juniperus virginiana*. Understory species included *Vinca minor* L., *Polygonum virginianum* L., *Vitis rotundifolia*, *Smilax glocka* L., *Asplenium platyneuron*, and *Lonicera japonica*. *M. vimineum* cover was sparse and intermixed with several other plant species at this site, although a few small, moderately dense patches of *M. vimineum* were also present.

At JIR, the sample design consisted of 35 sample points arrayed across the patch boundaries and the edges of gaps within the patch. These included 6 transects of 3 sample points each arranged perpendicular to the long axis of the patch, with 25-m spacing between transects and sample points. Transects were also established across each of two gaps in the *M. vimineum* cover within the patch, consisting of 10 and 7 sample points, respectively, with 3-m spacing between sample points. The sample design at WBW consisted of 18 sample points chosen at random x-y coordinates within the patch. At BVR, I established two orthogonal transects across the boundaries of the patch. Each transect consisted of 10 sample points at 10-m spacing. The environmental variables evaluated at each sample point were canopy openness, litter mass, aboveground biomass of other plant species, and soil moisture, carbon and nitrogen content (%), pH, rock content (%), and texture.

At each point, I measured soil moisture with a hand-held time domain reflectometer (Hydrosense, Decagon Devices, Pullman, WA, USA). I estimated

canopy cover (%) with a concave spherical densiometer. I then collected aboveground vegetation and leaf litter from within a round 0.25 m^2 quadrat at each point. Finally, I collected the upper 2 cm of mineral soil from a 15-cm diameter circle in the center of the quadrat.

In the laboratory, I separated *M. vimineum* from other plant taxa in each vegetation sample and identified those other taxa. I measured the height of the tallest *M. vimineum* shoot in each sample, and then oven dried all vegetation and litter samples at 60°C to constant mass.

Soil samples were air dried in the laboratory, then sieved to remove roots and rock fragments >2 mm. I used a graduated cylinder to estimate the proportional volumetric contribution of rock fragments to each soil sample. The pH of each soil sample was determined by combining equal volumes of air-dried, sieved soil and distilled water and measuring the pH of the slurry with an Orion SA720 pH meter (Orion Research, Inc., Beverly, MA, USA). Soil texture was determined for each sample using the texture-by-hand method. Each soil sample was analyzed for total nitrogen and total carbon with a LECO 2000 carbon, nitrogen, and sulfur autoanalyzer (LECO Corp., St. Joseph, MI) following the methodology of Matejovic (1997).

Statistical Methods

For the detailed site characterizations, I used a fixed-effects analysis of variance to determine site-specific differences for each environmental variable. I used Tukey's means separation test to test for differences among means (α=0.05).

Data for *M. vimineum* biomass and height were log transformed to correct departures from normality. However, reported means are always non-transformed data.

I used stepwise multiple regression (Zar 1999) to develop a predictive model of *M. vimineum* height and biomass in response to the measured environmental variables for all sites combined and each site individually. The threshold for retaining independent variables was α=0.15. Polynomial regressions were also conducted and evaluated for improvement of fit (i.e., increase in adjusted model R^2) over linear models (Zar 1999). These regressions were intended to assess performance, rather than presence/absence of *M. vimineum*, so only data from sample points where *M. vimineum* was present were included in the analysis.

I used logistic regression to develop models for predicting the odds of *M. vimineum* being present based on the measured environmental variables for all sample points. I performed collinearity diagnostics for all regressions; when two or more variables were highly autocorrelated, only the variable with the highest partial-R^2 was retained in the model.

Results

Landscape Level Distribution of *M. vimineum*

M. vimineum is distributed nearly continuously along all of the >50 km of roads within the Research Park, with the exception of areas that are maintained by mowing or herbicide application (e.g., power line crossings and highway rights-of-way). I found 24 locations where *M. vimineum* extended from a roadside into adjacent, usually understory, habitat. Many of these patches were in floodplains and

riparian zones, especially near river embayments. I also found six isolated, upland patches >1 m^2 in size that were at least 50 m from any road or established trail. *M. vimineum* is notably infrequent in the Walker Branch Watershed compared to other areas of the Research Park, and occurred as a narrow strip along some gravel roads, as sparsely distributed individuals on a few mounds created by uprooted trees, and along ephemeral watercourses. The only patch of *M. vimineum* >1 m^2 within the Walker Branch Watershed research area was at WBW.

The collection of 30 patches (i.e., the 24 roadside patches and the 6 upland patches) was highly variable in areal extent and ranged from <10 m^2 to several hectares. Based on a total of 90 samples (i.e., one sample from each of 27 of the 30 patches--3 patches were disturbed by machinery or road maintenance activities before they could be sampled-- plus a total of 73 sample points at the 3 intensively sampled sites), the maximum density of *M. vimineum* was 872 plants/m^2 (mean ± 1 SE = 361 ± 27), and aboveground biomass was as high as 877 g/m^2 (137 ± 19). The tallest individual plant observed was 185 cm (63 ± 4, shoot length).

Most of the *M. vimineum* patches were in level areas, but I occasionally found it on steep slopes and the nearly vertical sides of sinkholes. Although *M. vimineum* was observed in habitats that ranged from 0 to 100% open overstory canopy, most patches were found beneath overstory tree canopies that were about 5% open. Plant species composition was similar at all sites and was characteristic of mixed mesophytic hardwood forest with remnants of pine plantations (Barbour and Billings 1998).

With few exceptions, land use history was similar for all 30 patches. A variety of agricultural practices, especially logging, row crops, and pasture, had occurred throughout the Research Park until about 1940. Since that time, forest management has been the primary land use activity conducted across these sites. One site (BVR) was clearcut 2 years before this survey was conducted.

Soils beneath *M. vimineum* ranged in texture from loamy sand to clay loam, with pH values ranging from 4.4 to 6.5 (mean ± 1 SE = 5.6 ± 0.7). Total carbon in soils supporting *M. vimineum* ranged from 1.8% to 15.7% (5.1% ± 0.3%), and total nitrogen in those soils ranged from 0.12% to 0.55% (0.29% ± 0.01%). The volumetric water content of soils that supported *M. vimineum* ranged from 13% to 46% (25% ± 1%). Litter mass ranged from 400 to 6,998 g/m^2 (1,337 g/m^2 ± 171 g/m^2), and biomass of other plant species ranged from 0 to 434 g/m^2 (36 g/m^2 ± 11 g/m^2).

Detailed Site Characterization

Environmental characteristics differed among sites (Table 1). BVR had the most open canopy, and WBW had the most closed canopy. Soils at WBW and BVR were drier than at JIR. Soil pH was greater at WBW than at either JIR or BVR. Soil carbon and rock content, and litter mass and biomass of other plant species, were greater at BVR than at JIR and WBW. *M. vimineum* height and biomass were greatest at BVR.

Stepwise regression of the pooled data set from all three sites indicated that the best model for predicting *M. vimineum* biomass included only canopy openness and biomass of other plant species (Table 2). *M. vimineum* biomass was positively

related to canopy openness and negatively related to biomass of other plant species. *M. vimineum* height was positively related to canopy openness, and was inversely related to soil pH and the biomass of other plant species.

M. vimineum biomass at JIR was positively related to canopy openness and litter mass and negatively related to soil nitrogen content and biomass of other plant species (Table 2). At WBW, *M. vimineum* biomass was positively related to soil pH, carbon, and rock content and was negatively related to litter mass and biomass of other plant species. *M. vimineum* height at WBW was positively related to soil carbon and pH and negatively related to litter mass. At BVR, *M. vimineum* biomass was negatively related to soil pH, and height was positively related to soil nitrogen and rock content, while being negatively related to soil pH and litter mass. Differences in site characteristics (Table 1) and the relationships between dependent and independent variables from site to site are the likely explanation for the relatively low predictive power of the all-sites models and the inconsistencies in regression models from site to site (Table 2).

Logistic regression (data not shown) indicated that soil pH was the only environmental variable, among those measured, that could predict the presence of *M. vimineum*. Across sites, each unit increase in soil pH increased the odds of *M. vimineum* being present by a factor of 0.75 (i.e., an increase in odds from 1:1 to 1.75:1).

Discussion

Within the Research Park, *M. vimineum* exhibits the broad environmental tolerance of many "weedy" species. It is widely distributed throughout the Research Park, in habitats ranging from open to closed canopy sites, from level areas to steep slopes, from floodplains to upland habitats, and from recently disturbed roadways to intact forest. I observed a very complex pattern of distribution and abundance that included large, dense patches with abrupt edges as well as sparsely distributed individuals within diverse plant communities. The characteristics of sites that supported this species were comparable to those reported for invaded habitats in Maryland (Redman 1995).

Environmental Factors Correlated With Performance

Canopy openness and the biomass of other plant species were the most important variables that explain the performance of *M. vimineum* across the Research Park. Other researchers have noted that this species responds positively to increases in light availability (Horton and Neufeld 1998, Williams 1998, Barden 1996) in spite of observations that it is shade tolerant. While overstory canopy may facilitate *M. vimineum* establishment via improvement in water relations and protection from temperature extremes (Chapter 3, Holmgren et al. 1997), deep shade suppresses this species (Chapters 3 and 4).

The negative correlation between *M. vimineum* biomass and the biomass of other plants at JIR and for all sites combined suggests that interference or competition is occurring between *M. vimineum* and other plant species. Although there are

numerous anecdotal and qualitative accounts of negative interactions between *M. vimineum* and other plants, there are no published data. This study was not designed to evaluate direct inter-specific interactions. Experimentation would be required to determine whether *M. vimineum* suppresses the growth of other species or vice versa.

Soil pH was another important environmental variable related to *M. vimineum* performance; however the nature of the relationship between pH and growth response varied across sites (Table 2). Soil pH was positively related to *M. vimineum* height and biomass at WBW, whereas there was a negative relationship between pH and height and biomass at BVR. In the all-sites model, pH was negatively related to height. In comparison, Kourtev et al. (1999) reported that soils that supported *M. vimineum* were higher in pH than soils under native vegetation.

The ecological explanation for the negative relationship between *M. vimineum* growth response and litter mass at some sites is unclear. Litter might inhibit establishment of *M. vimineum* seedlings through reduction of light at the soil surface (Agee 1973). Alternately, litter might prevent dispersed seeds from contacting mineral soil, or reduce infiltration of rainwater to the surface soil (Helvey 1964). Release of allelopathic substances and changes in soil nutrient status caused by decomposing litter are additional plausible mechanisms by which litter may suppress *M. vimineum* (Xiong and Nilsson 1997).

Soil moisture did not appear in any of the regression models, which was surprising in light of reports that link *M. vimineum* invasion to moist habitats (Cusick 1986, Barden 1987, Redman 1995, Williams 1998, Mehrhoff 2000). A single measurement of soil moisture at each sample point might have been insufficient to

evaluate the importance of this environmental variable to *M. vimineum* performance throughout a growing season.

Environmental Factors That Affect Presence/Absence

M. vimineum was absent from many apparently suitable locations, consistent with the findings of Redman (1995), who observed that many moist, shady locations in Maryland had not been invaded by *M. vimineum.* The absence of *M. vimineum* in habitat that has the same underlying geology, topography, and soil type as habitat that supported *M. vimineum* suggests that other more local environmental factors or seed dispersal limitations are responsible for this complex pattern. With the exception of soil pH, the environmental variables I measured are not good predictors of *M. vimineum* presence/absence. The increased odds of presence with increasing pH should be interpreted with caution in that soil pH measurements were restricted to the range of 4.4 to 6.5, and the odds of presence might not change outside that limited range.

Propagule dispersal is an important determinant of the spatial distribution of any plant species, and the absence of viable seeds might be the primary explanation for the current absence of *M. vimineum* in many locations. Unfortunately, the role of seed dispersal limitations in creating the patterns of presence/absence cannot be evaluated with these data. However, considering the high fecundity observed in this species (Barden 1987) and the ease with which it has been observed to disperse via water and animals (Mehrhoff 2000) and as a contaminant in topsoil and mulch (NPS 1999), it is unlikely that dispersal is the only factor constraining the distribution of this species to its current pattern on the landscape. A recent seed bank study

confirmed that *M. vimineum* seeds can disperse up to 1 m on a level site within 3 months of release (Chapter 4). Despite the potentially important role of dispersal in the distribution and abundance of this species across the landscape, no other research has been conducted on the role of dispersal for this species. This is in particularly stark contrast with many other studies that focus on dispersal for other important plant invaders (cf Cronk and Fuller 1995).

Interactions Between Factors That Control Presence and Performance

Different environmental factors appear to control the performance of *M. vimineum* in different locations (Table 2). I suggest that the complex pattern of *M. vimineum* distribution and abundance that I observed in the Research Park is the result of seed dispersal limitations and this species' response to several spatially and temporally variable resources. Most natural systems exhibit a complex gradient of various resources, with some factors changing for the better and others changing for the worse with regard to the performance of any particular species; it is the net effect of these correlated changes that affect plant survival and growth Holmgren et al. (1997). Along any particular transect, the availability of any single resource (e.g., light) might not change appreciably, but small, simultaneous shifts in two or more resources (e.g., light and water) could be sufficient to create a patchwork of suitable habitat interspersed with habitat that is at least temporarily unsuitable. Thus, soils that are too dry to support *M. vimineum* under very low light conditions might be suitable habitat for this species under slightly higher light levels created by disturbance. A related model was proposed by Tilman (1982), whereby multiple

resource gradients and the differential ability of species to compete for each resource might account for plant community structure.

Research on the distribution and performance of prickly lettuce (*Lactuca serriola* L.) in Great Britain (Carter and Prince 1985, Prince et al. 1985, Prince and Carter 1985) demonstrated how environmental constraints and dispersal limitations can interact to create complex patterns of a species' distribution and performance. Carter and Prince (1985) noted an unusually abrupt limit to the altitudinal distribution of *L. serriola* and concluded that subtle climatic changes were responsible for that pattern. However, transplant experiments confirmed that *L. serriola* could survive beyond its distributional limit (Prince and Carter 1985). Although they found no marked decline in vigor of *L. serriola* toward its limits, these researchers concluded that even a small decline in the performance of individual plants, or in the availability of its preferred habitat, may produce a distribution limit that is abrupt relative to the environmental gradients that cause it (Carter and Prince 1985).

Similar studies of *M. vimineum* habitat in other portions of its introduced range are needed to evaluate the generality of these results. Experiments are needed to better quantify the growth response of this species to environmental variation, especially with regard to potential interactions among environmental factors (e.g., Chapter 3). Seed bank/seed dispersal studies are needed to evaluate the role of seed dispersal relative to environmental variation in determining the spatial distribution of this species (Chapter 4). Comparative studies of this species in its native range should be conducted to assess the degree to which its habitat and pattern of distribution coincide with those in its introduced range. The results of such studies

might reveal environmental or biotic factors (e.g., pathogens or herbivory) that limit its abundance in its native range.

CHAPTER 3

DEMONSTRATION OF A LIGHT/WATER TRADE-OFF IN *MICROSTEGIUM VIMINEUM*

Introduction

All plants require light, water, and nutrients for survival and growth (Maximov 1929, Franck and Loomis 1949, Rabinowitch 1956, Hall 1977, Turner and Kramer 1980, Blankenship 2002). In contrast to conceptual models that suggest that plant survival and growth are dependent on a single limiting resource (Leibig 1840), some of the earliest ecologists recognized the importance of interactions between environmental factors (Kreusler 1885, Clements and Shelford 1938, Odum 1953). In fact, the effect of one resource on plant performance is rarely independent of other resource levels (Chapin et al. 1987, Osmond et al. 1987). This suggests that resource interactions influence both plant population dynamics and community structure.

Plant resources may be mutually substitutable, wherein an increase in one resource can compensate for a decrease in the other resource (MacArthur 1972, Tilman 1982, Tilman 1997). When two resources are perfectly substitutable, plant performance (i.e., survival or biomass accumulation) is unaffected by a unit decrease in one resource given an equivalent increase in the other resource (Figure 1, line E). However, substitutable resources might not exhibit an interactive effect on plant performance. The linear nature of the zero growth isocline indicates that resource substitution is constant across all resource ratios and there is no interactive effect of the two resources on plant growth.

An alternative model of resource substitution, the trade-off model, has been proposed (Smith and Huston 1989, Holmgren et al. 1997). In the trade-off model, two plant resources are substitutable but also exhibit an interactive effect on plant growth (Figure 1, line F). The curvilinear zero growth isocline reflects the interactive effect of the two resources on plant growth, in that the magnitude of resource substitution changes with changing resource levels. For example, resource substitution is 1:1 (i.e., perfectly substitutable) when both resources are equally abundant. As the availability of either resource decreases, the amount of the other resource needed to maintain constant biomass increases at an increasing rate. Although considerable research has been devoted to resource substitution alone and resource interaction alone, the trade-off model that incorporates both resource substitution and resource interaction is far less understood. But, it has clear ramifications for the response of species where multiple important resources may vary concurrently in space and time.

A particular trade-off model has been hypothesized for light and water, whereby the effect of drought is exacerbated by low light and vice versa, and two mechanisms have been proposed to explain this potential response (Smith and Huston 1989, Holmgren et al. 1997). First, a plant growing in shade tends to invest proportionally more biomass to shoots, with a consequent increase in transpiration surfaces relative to roots, increasing the plant's vulnerability to drought. Alternatively, under dry conditions, a plant allocates more of its total biomass to roots, increasing the ratio of respiring biomass to photosynthetic tissue and shifting the whole-plant light compensation point upward, increasing the plant's light

requirement to offset energy losses to respiration. The second mechanism involves reduced stomatal conductance to avoid water loss under dry conditions, with subsequently reduced carbon assimilation. In this case, higher light levels are required to increase the photosynthetic rate while stomates are open.

Several studies have found evidence of interactive effects of light and water on plant growth (Vitousek and Denslow 1986, Kolb et al. 1990, Fisher et al. 1991, Dale and Causton 1992, Veenendaal et al. 1996, Baruch et al. 2000). However, these studies did not explicitly discuss their results in terms of a light/water trade-off. There have been three recent explicit tests of the light/water trade-off hypothesis (Holmgren 1996, Holmgren 2000, Sack and Grubb 2002). Although these studies did not detect any interactions between light and water, they lacked adequate experimental control or did not included a wide range of light and water levels. For example, field and greenhouse experiments conducted by Holmgren (1996, 2000) did not detect a trade-off in *Liriodendron tulipifera*, a tree species that is both shade- and drought-intolerant, but these experiments may not have included high enough levels of either light or water to demonstrate a potential trade-off. A recent experimental test of the light/water trade-off by Sack and Grubb (2002) found no interaction between light levels and water treatments on seedling mass, relative growth rate, or biomass allocation in any of four shade-tolerant, woody species. However, their study included only two light treatments and two water treatments, and they suggested that the watering treatments may have produced differences in soil nutrient status that confounded the results. Furthermore, all three of these studies used slow growing perennial species and tested for treatment effects on seedling performance

only. These design elements might have prevented the detection of a light/water trade-off.

I conducted a greenhouse experiment to test the light/water trade-off hypothesis using *Microstegium vimineum* (Trin.) A. Camus (Japanese grass), a shade-tolerant and drought-intolerant annual grass, as the test organism. My experimental design was intended to overcome some of the limitations associated with previous studies by (1) including the full range of light and water levels this species is likely to experience in a natural setting, (2) precisely manipulating these environmental variables, and (3) using an annual species to assess treatment effects over the lifetime of the organism. My objectives were to (1) determine if light and water are mutually substitutable resources in the case of *M. vimineum*, (2) determine if there is an interactive effect of light and water on the performance of this species, and (3) examine the role of shifts in root and shoot biomass allocation as a potential mechanism that controls its response to covarying resource levels.

Materials and Methods

Study Species

M. vimineum is a C_4 annual grass of Asiatic origin. It was first collected in the Western Hemisphere in 1919 in Knoxville, Tennessee (Fairbrothers and Gray 1972), and it is currently established throughout the eastern United States (Redman 1995). *M. vimineum* tolerates the low light typical of understory habitats yet maintains characteristics of plants adapted to high light environments, such as rapid induction loss and rapid stomatal movements in variable light (Horton and Neufeld 1998). It is

frequently observed at forest margins along roads and trails, as well as in floodplains and wetlands (Hunt and Zaremba 1992). The upper and lower photosynthetic thresholds for this species are 25% light and 5% light, respectively, (Winter et al. 1982). The moisture content of soil that supported *M. vimineum* in a field survey ranged from 13% volumetric water content (VWC) to 46% VWC (Chapter 2).

Experimental Design

I conducted a greenhouse experiment to investigate the response of *M. vimineum* to covarying gradients of light and water. *M. vimineum* plants were grown from seedlings to maturity in pots subjected to 5 levels of light and 4 levels of soil moisture in a randomized, fully crossed design. Light levels were established with shade cloth of different densities. Water levels were maintained by placing experimental units at set distances above a free and constant water table; blocks of a uniform porous medium set in the water column wicked water to the open-bottom pots. This technique maintained a constant soil moisture content (proportional to the distance between the bottom of the pot and the surface of the water table) in the pot regardless of changes in plant growth rate (Snow and Tingey 1985).

Experimental Units and Planting Protocol

Each experimental unit consisted of a 2.5-liter pot, the bottom of which was removed and replaced with two layers of fine-mesh nylon filter fabric. I collected soil to a depth of 0.3 m from beneath a dense, uniform patch of *M. vimineum* in the Oak Ridge National Environmental Research Park in April 2001. The soil was screened to remove the few rock fragments >1 cm in diameter and was used to fill each prepared pot.

In April 2001, I collected 6-cm tall *M. vimineum* seedlings from the site where the soil used to fill pots was collected and transplanted 5 seedlings into each pot. Pots were watered daily and maintained outdoors under shade for 5 days; during this time, seedlings were replanted as necessary. Pots were then transferred to a greenhouse at the University of Tennessee, where they were shaded with one layer of 85% shade cloth for 5 days to acclimate to greenhouse conditions. I randomly assigned each pot to a light and water treatment (n=5).

Light Treatment Levels

The five light levels established for this experiment were 75%, 25%, 10%, 5%, and 2% of ambient light. A 10% light treatment was chosen as an intermediate value between the reported photosynthetic thresholds of 25% light and 5% light, respectively. A 2% light treatment was chosen to determine whether *M. vimineum* can survive at light levels below 5% light. The highest light level was the maximum that could be achieved in the greenhouse.

Light treatments were created by suspending commercially available shade cloth of different densities over support frames set on greenhouse benches. Each 1.3 m x 1.3 m x 3.3 m frame was constructed from 2-cm diameter polyvinyl chloride pipe, and the top and all sides of each frame were completely covered with shade cloth. Direct measurements of light using a ceptometer (Accupar, Decagon Devices, Inc., Pullman, WA, USA) near noon on a clear day were used to verify the target light level for each treatment.

Water Treatment Levels

The four soil moisture levels selected for this experiment were 40%, 30%, 20%, and 10% VWC, which encompasses the range likely to be experienced by this species in the field. Data from a pilot experiment indicated that 10% VWC in loamy sand was below the threshold for *M. vimineum* germination and early seedling establishment. Field capacity (i.e., the maximum water holding capacity of a soil after draining) for the loam used in this experiment was ~ 40% VWC. The 20% VWC and 30% VWC treatment levels were chosen as intermediate values between the expected lower threshold (i.e., 10%) for *M. vimineum* survival and field capacity for the soil being used.

Each pot was set on a block of uniform porous medium (10 cm x 12 cm x 23 cm floral foam blocks, Smithers-Oasis U.S.A., Kent, OH, USA) placed on end in a clean, 20-liter, plastic bucket containing tap water (cf Snow and Tingey 1985). By maintaining the water column in the bucket at a constant distance below the interface between the bottom of the pot and the top of the foam block, a constant soil moisture was achieved regardless of the transpiration rate of the plants. The water depths that corresponded to the target soil moisture levels were determined before the experiment was initiated.

Five pots assigned to each of the four soil moisture levels were placed at random at 30 cm spacing on each greenhouse bench. To account for unknown environmental gradients in the greenhouse, every 7-10 days throughout the experiment I re-assigned light treatments at random to benches, moved all

experimental units and their associated shade cloth layer(s) to the new bench positions, and re-randomized pots within each light treatment.

Monitoring

I measured soil VWC in each unit at least weekly using a time domain reflectometer probe (Hydrosense, Decagon Devices, Inc., Pullman, WA, USA). It was easier to maintain target soil moisture in the 40% VWC treatment, so I measured VWC less frequently in those experimental units. I made minor adjustments to water levels as necessary to maintain target VWC. In some cases, I temporarily removed a pot from the foam block to allow soil moisture to return to the target level.

I monitored seedling survival on a weekly basis, and I measured the height and number of stems of each live plant in June and July. By mid-July, the plants in all but the 2 darkest treatments had 10 or more stems per plant and had rooted at multiple nodes. Therefore, I discontinued measurements of height and stem number.

During the first 2 weeks of the experiment, I monitored air temperature in each light treatment. One temperature logger (Stow Away Tidbit, Onset Computer Corporation, Bourne, MA, USA) was placed on top of a dry block of Oasis floral foam on each greenhouse bench.

At experiment termination, I harvested aboveground and belowground biomass by washing soil from the root mass and clipping roots from shoots. All biomass samples were oven dried at 50°C to constant mass. Roots were ashed at 500°C for 6 hours; root data are expressed as ash free root biomass.

Statistical Methodology

All biomass data were analyzed on a per plant basis to account for mortality.

I assessed the normality and homoscedasticity of all data sets and log-transformed data as appropriate. I used a two-way ANOVA model to examine differences in aboveground, belowground, and total (i.e., root plus shoot) biomass and root/shoot ratios at experiment termination, and a one-way ANOVA to compare minimum, maximum, and mean air temperature among light treatments. I used a Tukey means separation test to determine differences among means (α=0.05). I standardized the treatment levels to a common mean and standard deviation to account for differences in scale, estimated the per unit change in plant response to each resource, and used a one-way ANOVA to test for a difference between the unit response to light (i.e., gram of biomass increase per percent increase in light) and the unit response to soil moisture (i.e., gram of biomass increase per percent increase in VWC). A repeated measures analysis of variance (ANOVA) was used to analyze VWC data and test for flatness and parallelism of the response curves (von Ende 1993). A dependent t-test was used to compare the levels of the VWC response curves and determine if four distinct water treatment levels had been achieved.

Results

Plant Production, Allocation, and Survivorship

There was an interactive effect of light and water on root, shoot, and total biomass accumulation (Table 3), and the two resources are somewhat mutually substitutable in this species. Water treatment did not affect total biomass at 2% or at 10% light, whereas there was greater biomass accumulation in the higher water treatments at every other light level (Table 4). ANOVA of the growth response to

each percent increase in light versus water (standardized to a common mean) demonstrated that increasing light within water treatments had an even greater effect than increasing water within light treatments (p=0.005). Aboveground biomass reflected the same pattern as total biomass (Table 5). In contrast, there was less difference in belowground biomass across light treatments within water treatments or across water treatments within light treatments (Table 6). Root:shoot ratios were affected by the light treatment only (Table 3). Root:shoot ratios were greater in the 2% (mean ± 1 SE = 0.31 ± 0.06) and 10% (0.21 ± 0.05) light treatments than the other light treatments, which did not differ (Table 7).

Comparison of first- and second-order regression models fit to the total biomass data supports the trade-off. The first-order model containing only the linear terms for light and water yields R^2=0.5 (p<0.0001), whereas the second-order model containing only the light*water interaction term is a better fit to the data (R^2=0.63, p<0.0001). The relationship between these resources and plant growth is better depicted by the trade-off model (Figure 1, line F) than the model for resource substitutability without interaction (Figure 1, line E).

M. vimineum survivorship did not differ within light or water treatments (Table 3). Survival was >84% in all except the 10% VWC/ 75% light treatment. All plants in this treatment died early in the experiment when greenhouse temperatures suddenly increased and soils in the 10% VWC treatment dried down to the target level (or below, depending on the pot). Three of the five plants in one pot in the 30% VWC/ 10% light treatment died early in the experiment from unknown causes. Two large plants, one in the 25% VWC/ 40% light treatment and one in the 75% VWC/

20% light treatment, were accidentally uprooted late in the experiment and subsequently died.

At the end of the experiment, there was a striking difference in the appearance of plants in different light treatments. Plants in the highest light treatment were highly branched and beginning to show signs of early senescence or sun damage. Plants in the 5% light treatment were much smaller and exhibited minimal branching. Plants in the 2% light treatment were small, etiolated, and chlorotic. Biomass of plants that died prematurely was included in reported means for treatment groups.

Trends in Experimental Soil Moisture

Soil moisture contents varied over time, depending on the light and water treatments (time*water*light interaction, $p<0.0001$), especially early in the experiment (Figure 2). However, during the period of most rapid plant growth (i.e, between day 20 and day 50), water contents were relatively constant within light and water treatment combinations. Toward the end of the experiment, all water treatments exhibited a general drying trend. In spite of this variation over time, the four water treatments were different ($p<0.0001$).

Light Treatment Effects on Temperature

Minimum air temperature did not differ between light treatments ($p=0.92$), but mean air temperature was greater in the 75% light treatment (30 ± 1.6°C) than in any of the other light treatments ($p<0.0001$), which did not differ ($p>0.05$, 23 ± 0.5°C to 25 ± 0.7°C). Maximum air temperature was greater in the 75% light treatment than in the 25% light treatment, greater in the 10% light treatment than in the 5% light

treatment, and greater in the 25% light treatment than in the two lowest light treatments ($p<0.0001$, data not shown).

Discussion

These results support the light/water trade-off in *M. vimineum*. There is an interactive effect of light and soil moisture on aboveground and total biomass accumulation through the growing season. Light and water are mutually substitutable in this species, because plants grown in low light attained greater biomass when provided with more water, and plants grown in drier soils attained greater biomass when provided with more light (Table 4). For example plants grown at the reported lower photosynthetic threshold for this species (i.e., 5% ambient light) acquired almost twice as much biomass in the 20% VWC group compared to the 10% VWC group. However, this is not a perfect substitution, because light is a better substitute for water than water is a substitute for light.

Mechanisms That Control Light/Water Trade-offs

A shift in biomass allocation between roots and shoots is one of the proposed mechanisms for the light/water trade-off (Smith and Huston 1989), but this does not appear to be the mechanism in the case of *M. vimineum*, because there was little difference in root:shoot ratios among treatments. The higher root/shoot ratios in the 2% and 10% light treatments compared to the other light treatments were surprising, considering the often reported tendency for root/shoot ratios to be higher when soil moisture is limiting and lower when light is limiting (Bazzaz 1998). Perhaps shifts in

root:shoot allocation are less likely to occur in a fast-growing, annual species such as *M. vimineum.*

The findings of Horton and Neufeld (1998) support Smith and Huston's (1989) hypothesis that reductions in photosynthetic activity caused by reduced stomatal conductance under dry conditions are off-set by enhanced photosynthetic rate at higher light. They grew *M. vimineum* under 25% and 50% ambient light and measured the photosynthetic responses to both steady state and variable light. They found that plants grown in the higher light environment had higher maximum steady state photosynthetic rates compared to plants grown in the lower light environment. They also found that stomatal closure was very rapid in both groups of plants upon return to low light, but more rapid in those plants grown in higher light. Thus, it appears that *M. vimineum* is able to compensate for low soil moisture when light is abundant by taking advantage of the enhanced photosynthetic rate and more rapid stomatal closure at higher light levels. Conversely, its ability to take advantage of sunflecks through rapid induction increases its carbon gain in understory environments, so long as there is ample soil moisture to compensate for increased stomatal conductance in the low light environment.

Limitations on Tests of the Light/Water Trade-off Hypothesis

It is likely that light and water have an interactive effect on other plant species as well. Experimental design problems, rather than the absence of a trade-off, might have led other researchers to conclude that a light/water trade-off was not operating in their test species (Holmgren 1996, 2000, Sack and Grubb 2002). In particular, short-term (e.g., 1-year) experiments involving slow-growing perennial species are less

likely to detect a trade-off than experiments of sufficient duration to assess the effects of resource levels over the lifetime of the test organism. Furthermore, it would be difficult to detect a trade-off in plant species that are either tolerant, as in *Hedera helix* used by Sack and Grubb 2002, or intolerant, as in *Liriodendron tulipifera* used by Holmgren (1996, 2000) of both shade and drought. The functional groups considered by Smith and Huston (1989) in developing the trade-off hypothesis were either tolerant of low levels of one resource or were moderately tolerant of low levels of both resources, as in the case of *M. vimineum.*

Limitations on Resource Substitution in *M. vimineum*

An increase in soil moisture above 20% VWC did not cause an increase in biomass accumulation regardless of light level, suggesting that 20% VWC is at or near the optimal soil moisture for *M. vimineum* in this soil type. In the lowest water treatment, there was no increase in biomass as light increased above 10% light, which seems inconsistent with reports that the photosynthetic response of this species saturates at 25% light (Winter et al. 1982). However, photosynthesis may be limited by the availability of water at 10% VWC and would saturate at a lower threshold of light (Hopkins 1999). Plants grown in 2% light failed to grow in any water treatment.

There were unavoidable differences in air temperature created by the different light treatments, and the higher air temperature in the highest light treatment was a likely contributor to the mortality of all plants in the highest light/lowest water treatment. Plant water status is affected by thermal stress and transpiration demands as well as soil moisture (Barbour et al. 1999), and the combination of low soil moisture and high light and heat in this particular treatment combination, apparently

exceeded the physiological tolerance of *M. vimineum*. Clearly, resource substitution in this species is limited by the confounding effects of temperature on plant survival.

Conclusion

Light and water are mutually substitutable resources in *M. vimineum*, and there is an interactive effect of these resources on aboveground, belowground, and total biomass. This combination of resource substitution and interaction was described as a light/water trade-off by Smith and Huston (1989). Of the few explicit tests of this hypothesis, not one has successfully demonstrated such a trade-off until now. The light/water trade-off demonstrated in *M. vimineum* is likely operational in other plant species, but experiments that include a wide range of resources levels applied over the lifetime of the organism might be required to demonstrate it. Trade-offs between acquisition of light and water for plants growing under field conditions where either resource is likely to be limiting may have ramifications for plant population dynamics as well as community structure. Shifts in root and shoot allocation do not appear to be the mechanism of the trade-off in this species. Additional research is needed to test the alternative proposed mechanism involving stomatal conductance.

CHAPTER 4

ENVIRONMENTAL CONSTRAINTS ON THE DISTRIBUTION OF *MICROSTEGIUM VIMINEUM*

Introduction

The spatial distribution of plants in natural ecosystems is patchy at a wide range of scales, and the mechanisms that give rise to such patterns have been a central focus of the field of ecology. Spatial pattern is the result of past processes such as disturbance (Crawley 1986) as well as ongoing processes such as competition (Keddy 2001), and it affects future processes with regard to the plants themselves and the other organisms with which they interact (Dale 1999). For example, the population dynamics of herbivores and pollinators are influenced by the size, spacing, and density of patches of vegetation on which they feed (Dale 1999). Similarly, plants of one species can suppress or facilitate the establishment of other plant species in the same habitat (Smith and Huston 1989). Spatial heterogeneity in environmental factors such as topography (Greig-Smith 1961), soil depth (Kershaw 1959), and soil nutrients (Galiano 1985) has been shown to be related to patterns of vegetation on the landscape.

A better understanding of the relationships between environmental characteristics and the spatial distribution of various plant species would facilitate management of natural areas. For example, the ability to predict which habitats are most vulnerable to the invasion of non-native species is of particular concern to land managers (Williamson 1996). Identification of environmental factors that constrain a

species' distribution to certain positions on the landscape could aid efforts to control the spread of non-native plants.

Microstegium vimineum (Japanese grass) is a non-native plant that exhibits a complex pattern of distribution in its introduced range (Cusick 1986, Barden 1987, Redman 1995, Williams 1998). *M. vimineum* exhibits the broad environmental tolerance of many "weedy" species and has been observed in habitats ranging from saturated wetland soils to rocky ridge-top areas (Redman 1995, Ehrenfeld 1999, Chapter 2). *M. vimineum* is frequently found in disturbed understory habitats along roadbanks, streambanks, floodplains, and nearby mesic forest (Barden 1987), yet it tends to occur in discrete patches on the landscape. Redman (1995) noted that, in Maryland, *M. vimineum* was not found in many apparently suitable locations. This suggests that propagule dispersal or certain environmental factors limit the distribution of this invasive grass and its ability to dominate native plant communities.

There are few data on the particular mechanisms by which *M. vimineum* invades native plant communities. Anecdotal evidence and the pattern of this species' distribution on the landscape suggest that its seeds are naturally dispersed by overland flow of stormwater (Mehrhoff, 2000). Some of the 100-1000 seeds produced by each plant may remain viable in the soil for at least five years (Barden 1987).

M. vimineum is slow to invade undisturbed vegetation but rapidly fills disturbed areas, where it often forms dense monocultures (Barden 1987). Survey data (Chapter 2) supports other researchers' observations that this species is shade-tolerant

(Barden 1987, Redman 1995, Williams 1999, Horton and Neufeld 1998). Although it has the C_4 photosynthetic pathway, it will grow under light conditions as low as 5% sunlight, and its photosynthetic response has been reported to saturate at 25% sunlight (Winter et al. 1982). However, there are no published data on the light threshold below which *M. vimineum* can grow, survive, and reproduce.

Despite the unknown limitations on the local distribution of *M. vimineum*, there exist closed-canopy stands of eastern deciduous forests that support dense stands of *M. vimineum* that may extend for hectares (Chapter 2). These patches often exhibit distinct boundaries and gaps in *M. vimineum* cover. For example, there is a particularly striking pattern of this species' absence beneath some understory trees (e.g., *Juniperus virginiana*) and shrubs (e.g., *Lindera benzoin*). One example of an understory plant that appears to inhibit *M. vimineum* is the small deciduous tree *Asimina triloba*. This clonal species often forms patches consisting of dozens of stems. In habitats that support both *M. vimineum* and *A. triloba*, dense *M. vimineum* cover often ends abruptly at the drip line of the *A. triloba* patch. I developed 5 hypotheses regarding the causes of this pattern. (1) *M. vimineum* seeds have not dispersed beneath the *A. triloba* canopy. (2) *A. triloba* produces chemical (i.e., allelopathic) substances that inhibit *M. vimineum* seed germination or seedling survival. (3) Soil texture or other characteristics of soil beneath *A. triloba* are unsuitable for *M. vimineum*. (4) Transpiration by the *A. triloba* canopy reduces soil moisture to levels that cannot support *M. vimineum*. (5) Light levels beneath the *A. triloba* canopy are too low to support *M. vimineum*.

I conducted 4 experiments to test these hypotheses. These included 2 greenhouse experiments designed to investigate the roles of seed disperal, allelopathy, and soil characteristics (Hypotheses 1 through 3), and 2 field experiments to examine the main and interactive effects of soil characteristics, water, and light (Hypotheses 3 through 5) in the creation of the observed pattern of *M. vimineum* distribution relative to *A. triloba.*

Methods

Site Description

Research was conducted at the Oak Ridge National Environmental Research Park, Oak Ridge, Tennessee, USA. The Research Park consists of eastern deciduous forest, upland mixed forest, streams, and reservoirs within the Department of Energy reservation at Oak Ridge in eastern Tennessee. The climate is relatively mild, with an average winter temperature of 6°C and an average summer temperature of 24°C. Mean annual precipitation is 1500 mm. Elevation ranges from 250 to 420 m above sea level. Bedrock is dominated by calcareous siltstones and limestones, including the Conasauga and Chickamauga Groups (Oak Ridge National Laboratory 2000).

M. vimineum is widely distributed throughout the Research Park and is a dominant understory plant species in many areas of the park (Pounds et al. 1993. Chapter 2). It often forms dense, nearly continuous patches that may extend for hectares (Drake et al. 2001). One such location is a narrow, north-south trending valley near Hickory Creek Bend, 3 km south of Oak Ridge National Laboratory (N35°54' W84°16'). *A. tribola* patches approximately 60 m^2 in diameter, each of

which contains 30-50 stems 0.3 m to 5 m tall, are scattered throughout the floodplain. Conspicuous gaps in *M. vimineum* cover occur beneath the *A. tribola* canopy, and few individuals of any plant species other than *A. triloba* are present in any of the patches. The overstory is dominated by *Platanus occidentalis* L., *Acer negundo* L., *Juglans nigra* L., and *Liriodendron tulipifera* L.

Direct measurements of photosynthetic active radiation (PAR) with a line-integrating ceptometer (Accupar, Decagon Devices, Inc., Pullman, WA, USA) near noon on a clear day in mid-May were 15 ± 2 (mean ± standard error) μmol m^{-2} s^{-1} inside of *A. triloba* patches, compared to 249 ± 132 μmol m^{-2} s^{-1} in the understory immediately outside *A. triloba* patches. Thus, *A. triloba* canopies reduce light to 6-7% of ambient, understory light. Understory light at this site is about 20% of full ambient sunlight, so light levels beneath the *A. triloba* canopy are about 1% of full ambient sunlight.

Role of Allelopathy and Dispersal — Greenhouse Experiments

In autumn 2001 and late winter 2002 I conducted two greenhouse experiments to test the roles of seed dispersal (Hypothesis 1), allelopathy (Hypothesis 2), and soil characteristics (Hypothesis 3) in creating the gaps in *M. vimineum* cover beneath *A. triloba* patches.

Pre-dispersal Seedbank and Allelopathy Experiment

Prior to dispersal of *M. vimineum* seeds from the 2001 growing season, I conducted a seedbank study by collecting surface soil from under *A. triloba* and from adjacent stands of *M. vimineum* and providing suitable conditions for *M. vimineum* seed germination. To test the role of allelopathy, I monitored the emergence,

survival, and growth of *M. vimineum* seeds added to soils collected from under *A. triloba* and from adjacent stands of *M. vimineum*.

At the Hickory Creek research site, I selected three representative patches of *A. triloba*. For each patch, I identified 4 concentric zones: the center 2 m^2 (Zone 1), a 1-m wide band adjacent to Zone 1 (Zone 2), a 1-m wide band inside the edge of the patch (Zone 3), and a 1-m wide band 1-2 meters outside the patch edge (i.e., within the nearest location that supported *M. vimineum*, Zone 4). In October 2001 (prior to *M. vimineum* seed dispersal, which occurs primarily in November and December), I carefully cleared leaf litter and collected the top 2 cm of soil from three 0.5 m^2 plots in each zone; soil samples from each zone were pooled to obtain four composite soil samples from each patch.

Soil samples were screened through 0.5 cm hardware cloth to remove any rock fragments, which were few, and the screened soil was divided into six equal subsamples. Each subsample was spread to a depth of 1 cm over a 5-cm base of potting soil within a 26 cm x 52 cm plastic tray perforated to allow water drainage. Trays were arranged on benches in a greenhouse at the University of Tennessee. To each of three randomly chosen trays from each set of six trays, I planted 100 *M. vimineum* seeds collected from the Oak Ridge National Environmental Research Park at the end of the 2000 growing season. This resulted in three duplicates of each treatment (seeded vs. not seeded) for each zone from each patch. To provide controls to evaluate the adequacy of growing conditions in the greenhouse, I also planted 100 seeds in each of three trays that contained only potting soil. All trays were kept thoroughly watered for 30 days while I monitored seedling emergence and

survivorship on a daily basis. I randomly reassigned tray positions on a weekly basis to account for any unknown environmental gradients in the greenhouse. At experiment termination, I harvested aboveground biomass and dried it to constant mass at 50°C.

Post-dispersal Seedbank Experiment

In February 2002, after seeds from the 2001 growing season had dispersed, I conducted a second greenhouse experiment to test the role of dispersal in contributing to a seedbank. Several large rain events (up to 10 cm per day) had occurred during the previous 2 months, so physical dispersal of seeds by water had likely been accomplished. There was no evidence of ponding or scouring that might have flushed seeds from the site. I collected soil from each of the 4 zones at each of the 3 patches as described above. Composite samples were screened, divided into 2 duplicates, and placed into trays in a manner similar to the previous experiment. Trays were arranged on benches in the greenhouse and were watered and monitored for emergence and survivorship daily for 28 days. No potting soil controls were included in this experiment, because greenhouse conditions were similar to those in the first experiment.

Role of Light, Water, and Soil Characteristics—Field Experiments

In summer 2001, I conducted two separate field experiments to examine the role of other soil characteristics (Hypothesis 3), soil moisture (Hypothesis 4), or light (Hypothesis 5) in creating gaps in the cover of *M. vimineum* under *A. triloba*.

Understory Canopy Removal Experiment

I released potential soil moisture and light constraints imposed by transpiration and shading, respectively, by removing the canopy from half of each of three patches of *A. triloba*. I then planted *M. vimineum* seedlings into subplots on the cut and uncut sides of the patches and the existing stand of *M. vimineum* outside the patches.

First, I removed all leaves from the *A. triloba* stems in the southern half of each patch. To minimize unintended increases in light on the uncut side of the patch, I suspended a 3-m screen of 80% shade cloth vertically across the center of each patch (Figure 1).

I established 4 experimental subplots (0.25 m^2 each) at random locations within the cut and uncut sides of each *A. triloba* patch. Two additional subplots were established in the existing *M. vimineum* stand 2-3 m from each patch. Subplots were cleared of litter and existing vegetation by hand and surrounded by poultry wire to minimize disturbance by vertebrates. Nine *M. vimineum* seedlings (8-10 cm tall, collected from the site on the day of planting) were transplanted into each sub-plot in mid-May 2001. All subplots were watered and re-planted as necessary for one week, although transplant mortality was low. All other plants were hand-weeded upon emergence during the course of the experiment.

Removal of the *A. triloba* canopy could release potential soil moisture constraints on *M. vimineum* by reducing transpiration. To separate potential effects of soil moisture from effects of light I affixed shade cloth over two of the four subplots in the cut side of each *A. triloba* patch to reduce light levels to those prior to canopy

removal (i.e., 6-7% of ambient understory light). To release potential soil moisture limitations on the uncut side, I watered two randomly chosen subplots in the uncut side of each patch weekly. Watering was equivalent to a 3-cm rain event or about 100% increase over mean summer precipitation (National Weather Service 2002).

Once plants were established, I monitored each individual for survival, height, number of stems, and fruit set until experiment termination in October 2001. I measured soil volumetric water content (VWC) monthly in each subplot using a hand-held time domain reflectometer (TDR) probe (Hydrosense, Decagon Devices, Inc., Pullman, WA, USA). I measured PAR in each subplot twice during the experiment. To evaluate potential treatment effects on surface soil temperature, I placed one temperature data logger (StowAway Tidbit, Onset Computer Corporation, Bourne, MA, USA) on the soil surface in the center of the cut and uncut sides of each *A. triloba* patch, and adjacent to the two subplots outside each *A. triloba* patch. Data loggers collected temperatures data hourly for the first two weeks of the experiment.

At experiment termination, I measured plant height, checked for seed set, and then harvested aboveground biomass by clipping each subplot at ground level. Biomass samples were dried at 50°C to constant mass.

Light Gradient Experiment

I conducted a second field experiment to determine lower thresholds of light to *M. vimineum* survival and growth. In May 2001, I established 16 1-m^2 plots in an existing stand of *M. vimineum* near the *A. triloba* experiment. Each plot was thinned by hand of *M. vimineum* (and the few other herbaceous species present) to leave 12 *M. vimineum* seedlings (about 10 cm tall) in the center 0.1 m^2 of each plot. One of 4

light treatments was assigned at random to each plot: full ambient understory light, and 40%, 16%, and 6% of ambient understory light. Light treatments were created by suspending layers of commercially-available shade cloth 30 cm above the plots on metal stakes. Seedlings were carefully monitored for mortality for the first week of the experiment to confirm that thinning had no adverse effect on the seedlings left in situ.

Plots were monitored monthly for *M. vimineum* survival until experiment termination in October 2001. I measured soil moisture monthly in each plot. I monitored temperature for the first 2 weeks of the experiment with temperature data loggers placed on the soil surface of two randomly chosen plots within each light treatment. At experiment termination in late October, I clipped aboveground biomass at ground level. Biomass samples were dried at 50°C to constant mass and were checked visually for the presence of seeds.

Statistical Analysis

I used fixed effects analysis of variance to analyze *M. vimineum* survivorship, height, and biomass data from the allelopathy and dispersal greenhouse experiments and the *A. triloba* and light gradient field experiments. *A. triloba* patches were treated as experimental units, with data averaged across duplicate subplots and sub-samples. I used Tukey's means separation test to determine which means were different (α=0.05). I also used ANOVA models to determine the effects of treatment on minimum, maximum, and mean temperatures, and soil moisture, in the *A. triloba* and light gradient field experiments.

I used single-degree of freedom constrasts to test specific hypotheses regarding treatment effects on *M. vimineum* survival, height, and biomass in the *A. triloba* field experiment. The following contrasts were performed: inside patch versus outside patch (Contrast 1), cut side versus uncut side (Contrast 2), subplots in the cut sides of patches with artificial shade versus those without artificial shade (Contrast 3), subplots in the uncut sides of patches that were watered versus those that were not watered (Contrast 4), and subplots outside the patch versus unshaded subplots in the cut sides of patches (Contrast 5).

Results

Role of Dispersal and Allelopathy

In the pre-dispersal greenhouse experiment, no *M. vimineum* seedlings emerged in any of the trays to which seed had not been added (Table 8). In the trays to which seed had been added, *M. vimineum* seedlings emerged 7-14 days after planting, and ≥ 80% of planted seeds germinated. All emerged seedlings survived the course of the experiment. There was no difference in seedling emergence (p=0.36) or biomass (p=0.66) among any of the zones, and there was no difference between any of the zones and the controls (Table 8).

In the post-dispersal experiment, emergence of *M. vimineum* from soil collected from outside patches was at least an order of magnitude greater (p=0.002) than from soil collected from any zone within patches (Table 8). Within patches, seedling emergence did not differ among zones.

Role of Light, Water, and Soil Characteristics

Understory Canopy Removal Experiment

Survival of *M. vimineum* was two times greater in subplots outside the *A. triloba* patches (93%) than the subplots within the patches (43%), and was almost 3 times greater in subplots in the cut sides of the patches (62%) than subplots in the uncut sides of the patches (24%) (Table 9). Survival in the cut sides of the patches was nearly 4 times greater in unshaded (98%) versus shaded (26%) subplots. Survival did not differ between watered and unwatered subplots in the uncut sides of the patches, or between subplots outside patches and unshaded subplots in the cut sides of the patches.

Biomass of *M. vimineum* was greater outside than inside patches, greater in cut sides than in uncut sides, and greater in unshaded than shaded subplots in the cut sides (Table 9). Biomass did not differ between watered and unwatered subplots in the uncut sides of patches or between subplots outside patches and unshaded subplots in the cut sides. Mean plant height was greater in subplots outside the patches (21 cm) than subplots inside the patches (17 cm). Every plant that survived to the end of the experiment produced seeds.

Daily minimum, mean, and maximum temperatures did not differ among cut sides, uncut sides, and outside patches ($p>0.07$, data not shown). There was no difference in soil moisture on any date ($p>0.4$, mean ± 1 SE = 23 ± 5% VWC) among any of the treatments.

Light Gradient Experiment

Survivorship of *M. vimineum* in unshaded plots throughout the growing season was 100% (Figure 3). At experiment termination, *M. vimineum* survival was greater ($p<0.0001$) in plots that received 60% ambient understory light than plots that received 16% and 6% ambient understory light, which did not differ.

Mean biomass per plant was at least 16 times greater ($p<0.0001$) in the ambient understory light treatment (0.66 g ± 0.05 g) compared to all other treatments, and was greater at 40% ambient (0.04 g ± 0.01 g) than the other two light treatments (0.0008 g ± 0.0003 g at 16% ambient; 0.005 g ± 0.005 g at 6% ambient), which did not differ ($p>0.8$). Every plant that survived to the end of the experiment produced at least one seed, including plants as small as 10 cm tall.

Soil moisture content did not differ among the four treatments ($p=0.19$, mean ± 1 SE = 23% ± 2%). In addition, minimum, mean, and maximum temperature did not differ among the light treatment levels ($p>0.12$, data not shown).

Discussion

I reject Hypothesis 2 that allelopathy is a cause of the absence of *M. vimineum* beneath the *A. triloba* canopy, because emergence, survival, and biomass accumulation of *M. vimineum* added as seeds in the greenhouse experiment did not differ between surface soil collected from inside or outside the *A. triloba* patches (Table 8). Allelopathy has not been reported for *A. triloba* by other researchers.

The apparent absence of viable *M. vimineum* seeds in soil collected from beneath existing stands of *M. vimineum* at the end of the 2001 growing season (before

that cohort of seeds had dispersed; Table 8) does not support reports that this species creates a persistent seed bank (Barden 1987) but does support more recent reports that the species does not create a seed bank (Williams 1998). In this case, it appears that all seeds from previous growing seasons had either germinated or died by the end of that growing season.

In late winter 2002 after seeds dispersed, I found far more viable *M. vimineum* seeds in soils that supported that species in the previous growing season compared to soils inside the *A. triloba* patches (Table 8). This tends to support Hypothesis 1 that *M. vimineum* is absent beneath the shrub canopy because of limitations on seed dispersal. However, seeds had dispersed up to 2 m into the *A. triloba* patches, which suggests that seed dispersal alone is an inadequate explanation for the lack of *M. vimineum* in all zones within the patch. This suggests that other mechanisms play a greater role than dispersal limitation in creating the pattern. No other investigations of the role of seed dispersal in constraining this species' distribution have been published.

I rely on two lines of evidence to reject Hypothesis 3 that differences in soil characteristics (e.g., texture or other physical or chemical properties) inside and outside patches are responsible for the absence of *M. vimineum* beneath the *A. triloba* canopy. First, seed germination and seedling survival and growth in the greenhouse were uniformly high and did not differ between soils collected from inside and outside the patches (Table 8). Second, *M. vimineum* plants in unshaded subplots inside the cut side of patches accumulated biomass equivalent to plants grown in the existing stand of *M. vimineum* (Table 9).

I cannot definitively reject Hypothesis 4 that soil moisture limitations are responsible for the absence of *M. vimineum* beneath the *A. triloba* canopy, because watering did not measurably affect soil moisture. Regardless of watering, survival and biomass did not differ in plots in the uncut sides of patches. The absence of a treatment effect in the watered subplots is probably because of abundant rainfall and relatively high soil moisture levels throughout the research site during the 2001 growing season. However, it is unlikely that soil moisture is an adequate explanation for the absence of *M. vimineum* beneath *A. triloba* canopy, because plants provided with 200% mean annual precipitation throughout the growing season had lower survivorship and biomass than plants grown in higher light without added water.

I cannot reject Hypothesis 5, that light levels beneath *A. triloba* are too low to support *M. vimineum*, because (1) survival and biomass accumulation of plants in unshaded subplots in the cut sides of *A. triloba* patches exceeded survival and biomass in the shaded subplots as well as subplots in the uncut sides of the patches, and (2) survival and biomass of plants in subplots outside the patch exceeded survival and biomass of plants in subplots within patches (Table 9). These results indicate that light reduction by *A. triloba* is the primary environmental factor that prevents establishment of *M. vimineum* beneath its canopy. This conclusion is further supported by the results of the light gradient experiment, in which seedling survival and growth was reduced by shade cloth that created light levels comparable to those beneath *A. triloba* (16% light treatment, Figure 3). In Chapter 3, I demonstrated that *M. vimineun* is incapable of surviving at 2% sunlight in the greenhouse, regardless of

soil moisture availability; 16% of ambient understory light at the Hickory Creek research site is about 3% of full ambient sunlight.

Other researchers have yet to report that low light *per se* inhibits the establishment of *M. vimineum* in certain habitats, but it has been often reported that disturbance or opening in existing vegetation is required for successful establishment and persistence of *M. vimineum* (Barden 1987, Hunt and Zaremba 1992, Redman 1995). Results of this research suggests that light limitation is the mechanism by which undisturbed vegetation limits the invasion of *M. vimineum.* This mechanism is, of course, dependent on the adequacy of seed dispersal, which is not likely to be limiting, considering the rapid spread of this species through the eastern United States in only about 80 years.

Conclusions

Results of the 2 greenhouse and 2 field experiments described here indicate that seed dispersal, soil characteristics, soil moisture, and allelopathy are insufficient to explain the abrupt discontinuity in *M. vimineum* cover at the edge of *A. triloba.* In contrast, light reduction by *A. triloba* is the environmental factor most likely to control the distribution of this non-native, invasive grass. This is likely to occur for other woody plants, and the breadth and extent of this phenomenon should be evaluated.

This is the first experimental investigation of the environmental constraints on the spatial distribution of *M. vimineum.* Improved understanding of the ecological mechanisms that create complex patterns of its presence and abundance should enable

land managers to predict which habitats are most vulnerable to invasion by this species and to enhance control efforts.

CHAPTER 5

CONCLUSIONS

Before I conducted this research, little was known about *Microstegium vimineum* in natural ecosystems. A few researchers had noted its rapid expansion of range since its introduction to North America early in the 20th century (Fairbrothers and Gray 1972, Cusick 1986, Hunt and Zaremba 1992, Mehrhoff 2000), and at least one study of its spatial distribution and habitat had been conducted (Redman 1995). Investigations of this species' response to different light environments (Winter et al. 1982, Barden 1996, Horton and Neufeld 1998, Williams 1998) and soil nutrients (Claridge 2000) had provided evidence of its broad environmental tolerance and plasticity. Less attention has been given to its ability to invade plant communities (Barden 1987) and change ecosystem properties (Kourtev et al. 1999). No investigations of environmental constraints on its distribution had been conducted.

Prioritization and effective control of this non-native, invasive grass has been constrained, in part, by inadequate knowledge of this species' environmental requirements. *M. vimineum* tends to occur in discrete patches on the landscape, and Redman (1995) noted that, in Maryland, *M. vimineum* was not found in many apparently suitable locations. This suggests that certain environmental factors, or interaction of factors, limit the distribution of this invasive grass and its ability to dominate native plant communities. The purpose of my research was to identify the environmental factor(s) that most influence the invasion success of *M. vimineum* and to quantify this species' growth response to different resource levels. I used a

combination of field surveys and field and greenhouse experiments to develop more detailed information regarding this species' spatial distribution and environmental factors that constrain it to certain habitats.

I began with a survey of the distribution of *M. vimineum* on a 5000-ha, forested landscape in the southeastern United States (Chapter 2). I documented that *M. vimineum* is widely dispersed throughout the Oak Ridge National Environmental Research Park and occurs in a variety of habitats ranging from open to closed canopy sites, from level areas to steep slopes, from floodplains to upland habitats, and from recently disturbed roadways to intact forest. Most of the habitat in which *M. vimineum* was established was in or near a road. Virtually all of the >50 km of unpaved roads within the Research Park supported dense stands of *M. vimineum*, and most of the other patches >1 m^2 were within a few meters of a road or highway. This pattern of spatial distribution indicates the importance of seed dispersal, disturbance, and light to the establishment of this species. Roads provide dispersal corridors for seeds in topsoil, mulch, and tracked in on vehicles and shoes. Also, roads are openings in both ground and overstory vegetation, and further disturbance of soil and vegetation tends to occur in proximity to roads as a result of human activity such as logging, farming, and residential or other development. Reduced competition or interference from other plants may increase the availability of resources, especially light and water, to this fast-growing invader. Due to the high fecundity of *M. vimineum* (Barden 1987, Williams 1998), a few introduced individuals have the potential to produce a dense patch within a few growing seasons. Once established,

M. vimineum appears to be capable of suppressing the growth of other plant species, although data are unavailable as yet to confirm this impression.

Within the Research Park, *M. vimineum* exhibits the broad environmental tolerance of many "weedy" species. However, the species was absent from many apparently suitable locations, consistent with the findings of Redman (1995) in Maryland. I observed a very complex pattern of distribution that included large, dense patches with abrupt edges and distinct discontinuities as well as sparsely distributed individuals within a diverse plant community. Soil pH was the best predictor of *M. vimineum* presence/absence, and canopy openness and other plant species biomass were the best predictors of the performance of this species across the Research Park, although different environmental variables were related to invasion success at individual sites. For example, my field experiments demonstrated that light reduction by the canopy of shrubs such as *Asimina triloba* prevents the establishment of this species in certain habitats.

The importance of soil moisture to the establishment of this species has been noted by other researchers, who have also commented on its frequent occurrence in low light environments (Barden 1987, Redman 1995, Horton and Neufeld 1998, Williams 1998, Mehrhoff 2000). My greenhouse experiment demonstrated that light and water are mutually, though not equally, substitutable resources in the case of *M. vimineum* (Chapter 3). Furthermore, light and water have an interactive effect on plant performance. This interaction is beneficial to the plant when both resources are abundant, but there is a trade-off in that the interaction is detrimental when both resources are scarce. The mechanism for this interaction is still unclear, but research

on the response of *M. vimineum* to sunflecks suggests that the physiology of this species enables it make efficient use of low, variable light as long as there is ample soil moisture to compensate for increased stomatal conductance in the low light environment. Unusual arrangements of the cells involved in C_4 photosynthesis in the leaves of *M. vimineum* (Ueno 1995) might be related to this species' success in understory environments. Conversely, it appears that *M. vimineum* is able to compensate for low soil moisture when light is abundant by taking advantage of the enhanced photosynthetic rate and more rapid stomatal closure at higher light levels (Horton and Neufeld 1998). However, the confounding effect of higher temperature at high light, combined with water stress, can be fatal to *M. vimineum* seedlings, as demonstrated in Chapter 3. Thus, it appears that facilitation via improvement in water relations and moderation of air temperature (Holmgren et al. 1997) enables this species to flourish beneath tree canopies.

Several observations from this research provide additional insight regarding life history traits that might relate to the invasion success of *M. vimineum*. The very high success rate in transplanting established seedlings was surprising for this annual grass, and the observed hardiness of these plants during three months of frequent handling is likely related to the ecological success of the species in its introduced range. Shoots were resistant to breaking, which suggests that they would withstand trampling, flooding, and other forms of physical disturbance. I observed that young seedlings, although easily uprooted, have a high rate survival rate when their exposed roots have access to loose, moist soil shortly after being uprooted. It light of these observations, it seems plausible that, although seeds are the primary mechanism of

spread, this species is capable of dispersing as seedlings, when disturbed by flooding or tracking by animals, humans, vehicles, or machinery.

The plasticity of growth form in response to light levels was another surprise, and such plasticity in this species had not been reported by other researchers. Young *M. vimineum* plants grown in high light conditions quickly develop multiple stems, often >10 per plant, and roots at nodes. Even plants grown in the field under low light conditions tend to root at multiple nodes, especially when grown at low densities with considerable bare soil available in the immediate surroundings (Chapter 4). This phenotypic plasticity might be related to the success of this species in invading and persisting in its introduced range. Even low-magnitude disturbance (e.g., death of a single tree) that increases the availability of light and/or bare soil in the vicinity of established *M. vimineum* plants or propagules is likely to increase biomass and cover of this species. Because greater biomass generally translates into greater fecundity for annual species (Silvertown and Charlesworth, 2001), this plastic response to even slight disturbance in one growing season may enhance the spread and persistence of *M. vimineum* in subsequent years.

This species tolerates a wide range of light and soil moisture conditions, and data from both field (Chapter 2) and greenhouse (Chapter 3) investigations suggest that the performance of this species can be largely explained by the interactive effect of light and water. However, field survey data (Chapter 2) reveal that several additional environmental factors are important predictors of distribution and abundance, namely biomass of other plant species, litter mass, and soil pH. Most natural systems exhibit a complex gradient of various resources, with some factors

changing for the better and others changing for the worse with regard to the performance of any particular species; it is the net effect of these correlated changes that influences plant survival and growth (Holmgren et al. 1997). This might be especially true in eastern deciduous forest systems, where changes in precipitation patterns and frequent small-scale disturbance that alters canopy characteristics from year to year can create a shifting mosaic of resource availability. I suggest that the asynchronous shifts between the availability of resources across a landscape might be the most realistic conceptual model of resource limitation for this species. Limitations on propagule dispersal might be the primary determinant of the distributional pattern of this species on a coarse (e.g., regional) scale, whereas the interaction of resources, especially light and soil moisture, appears to drive the finer scale pattern that can be observed at individual invaded sites (cf. Huston 2001).

The importance of maintaining undisturbed native vegetation is one of the conservation implications of these findings. My survey results are consistent with other reports that roads and trails are the most common habitats in which *M. vimineum* is found in its introduced range (Barden 1987, Hunt and Zaremba 1992, Redman 1998, Mehrhoff 2000); these linear gaps in forested systems appear to provide a corridor for the spread of this non-native species. Forest fragmentation by development, including agriculture, increases the amount of edge habitat that favors the establishment of *M. vimineum* and increases the opportunities for its invasion into nearby intact forest.

As second growth forests in the eastern United States mature, overstory canopy should become more closed, potentially reducing understory light to levels

below those that can support *M. vimineum*. Thus, an optimistic scenario is that *M. vimineum* is a temporary invader of second growth forests. An alternative scenario is that *M. vimineum* is displacing native plant species or changing ecosystem properties (Kourtev et al. 1999). Such ecosystem-level changes might facilitate further invasions by non-native species and allow invaders to persist (Simberloff and von Holle 2000). For example, the open understory at many of the sites that support large, dense stands of *M. vimineum* (Chapter 2) suggests that this fast growing annual grass is suppressing forest regeneration, perhaps by shading young tree seedlings.

Many questions remain regarding the ecological impacts of this species. Anecdotal reports that *M. vimineum* can displace native species in as little as 3 to 5 years should be investigated through field surveys and experimentation. Potential ecosystem-level changes, such as prevention of woody seedling recruitment, should be investigated with removal experiments. Recent research (Klironomos 2002) has shown that when plant community composition changes (as after invasion by a non-native species), the composition and structure of the soil microbial community might also change in a way that facilitates persistence of the invader(s) and prevents recolonization by displaced species. Research should be conducted to determine if this is one of the mechanisms by which *M. vimineum* is able to persist in invaded habitats. Projected increases in atmospheric carbon dioxide might change the nature of interspecific interactions such as competition, especially between a C_4 plant like *M. vimineum* and its C_3 neighbors, which could be determined through experimentation.

Furthermore, the physiological mechanism of the light/water trade-off in *M. vimineum* remains to be determined. Further experimental research should be

conducted to test the hypothesized mechanism of stomatal conductance. Comparative studies of the distribution, abundance, and ecological impacts of *M. vimineum* in its native and introduced ranges is one of the most pressing research needs with regard to this species.

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APPENDIX

Table 1. Mean ± 1 standard error, and range for several environmental characteristics of Jones Island Road (JIR, n=35), Bethel Valley Road (BVR, n=20), and Walker Branch Watershed (WBW, n=18) sites in summer 2000 in the Oak Ridge National Environmental Park, Oak Ridge, Tennessee

Site Characteristic		JIR	WBW	BVR
canopy openness (%)	mean	8 ± 2 a	3 ± 1 b	49 ± 8 c
	range	0 – 80	0 – 15	5 – 100
soil moisture (%VWC)	mean	26 ± 1 a	19 ± 1 b	20 ± 1 b
	range	11 – 43	13 – 32	10 – 46
soil pH	mean	5.3 ± 0.1 a	6.0 ± 0.2 b	5.4 ± 0.2 a
	range	4 – 6	4 – 8	4 – 7
soil carbon content (%)	mean	3.9 ± 0.3 a	5.3 ± 0.3 a	7.2 ± 0.8 b
	range	1.8 – 7.6	3.5 – 8.0	2.9 – 15.7
soil nitrogen content (%)	mean	0.26 ± 0.02 a	0.31 ± 0.02 a	0.30 ± 0.02 a
	range	0.1 – 0.5	0.2 – 0.5	0.1 – 0.6

Table 1. Continued

Site Characteristic		JIR	WBW	BVR
soil rock content (vol/vol; %)	mean	4 ± 1 a	9 ± 2 a	23 ± 3 b
	range	0 – 23	1 – 38	1 – 51
litter mass (g/m^2)	mean	1, 178 ± 116 a	842 ± 83 a	2,782 ± 523 b
	range	380 – 4, 032	404 – 1,712	548 – 8,618
other plant biomass (g/m^2)	mean	23 ± 5 a	26 ± 7 a	112 ± 31 b
	range	0 – 140	0 – 116	0 – 434
M.. vimineum shoot length (cm)	mean	32 ± 4 a	42 ± 5 ab	58 ± 11 b
	range	0 – 75	0 – 78	0 – 130
M. vimineum mass (g/m^2)	mean	29 ± 7 a	22 ± 6 a	108 ± 26 b
	range	0 – 156	0 – 84	0 – 344

Means with the same letter are not different ($p>0.05$).

Table 2. Linear regression summary for Jones Island Road (JIR, n=35), Bethel Valley Road (BVR, n=20), and Walker Branch Watershed (WBW, n=18) research sites in the Oak Ridge National Environmental Research Park, Oak Ridge, Tennessee, summer 2000

Site	Response Variable	p-value	Model R-square	Model	Independent Variable	Partial R-square
All	Biomass (g/m^2)	0.002	0.25	$y = 1.2 + 0.03 X_1 - 0.006 X_2$	X_1 = canopy openness	0.10
					X_2 = other plant biomass	0.15
	Height (cm)	0.0002	0.36	$y = 2.0 - 0.08 X_1 + 0.01 X_2 - 0.001 X_3$	X_1 = soil pH	0.17
					X_1 = canopy openness	0.12
					X_3 = other plant biomass	0.07
JIR	Biomass (g/m^2)	0.008	0.50	$y = 1.4 - 3.1 X_1 + 0.1 X_2 - 0.02 X_3 + 0.0004 X_4$	X_1 = soil nitrogen	0.12
					X_2 = canopy openness	0.20
					X_3 = other plant biomass	0.12
					X_4 = litter mass	0.06

Table 2. Continued.

Site	Response Variable	p-value	Model R-square	Model	Independent Variable	Partial R-square
WBW	Biomass (g/m^2)	0.001	0.94	$y = -1.6 + 0.3\ X_1 + 0.5\ X_2 + 0.01\ X_3 - 0.01\ X_4 - 0.002\ X_5$	X_1 = soil carbon	0.11
					X_2 = soil pH	0.12
					X_3 = soil % rock	0.03
					X_4 = other plant biomass	0.10
					X_5 = litter mass	0.58
	Height (cm)	0.004	0.08	$y = 1.1 + 0.1\ X_1 + 0.1\ X_2 - 0.0007\ X_3$	X_1 = soil carbon	0.17
					X_2 = soil pH	0.12
					X_3 = litter mass	0.51
BVR	Biomass (g/m^2)	0.04	0.38	$y = 4.7\ 0.5\ X_1$	X_1 = soil pH	0.38

Table 2. Continued.

Site	Response Variable	p-value	Model R-square	Model	Independent Variable	Partial R-square
	Height (cm)	0.002	0.93	$y = 2.4 + 2.9\ X_1 - 0.3\ X_2 + 0.02\ X_3 - 0.00007\ X_4$	X_1 = soil nitrogen	0.24
					X_2 = soil ph	0.29
					X_3 = soil % rock	0.27
					X_4 = litter mass	0.13

Notes: Regression model for height at JIR not significant ($p>0.05$). Independent variables considered for each model included canopy openness, litter mass, biomass of other plant species, soil pH, and soil moisture, rock, carbon, and nitrogen content.

Table 3. ANOVA summary table, *Microstegium vimineum* light/water trade-off experiment, 2001

Factor	Survival	Total biomass	Shoot mass	Root mass	Root:shoot
Light	0.31	<0.0001	<0.0001	<0.0001	<0.0001
Water	0.55	<0.0001	<0.0001	<0.0001	0.13
Light*Water	0.59	<0.0001	<0.0001	0.04	0.78

Table 4. *Microstegium vimineum* total biomass (g/plant; mean ± 1 standard error) at termination of light/water trade-off experiment

Light (%)	Target Volumetric Water Content (%)			
	10	20	30	40
2	0.04 ± 0.003 Aa	0.05 ± 0.004 Aa	0.04 ± 0.005 Aa	0.05 ± 0.004 Aa
5	0.18 ± 0.04 Aa	0.34 ± 0.03 Aab	0.48 ± 0.09 Ab	0.43 ± 0.08 Aab
10	1.09 ± 0.08 Ba	1.8 ± 0.2 Ba	2.13 ± 0.4 Ba	1.82 ± 0.6 ABa
25	1.4 ± 0.2 Ba	2.08 ± 0.4 BCb	3.06 ± 0.2 BCb	3.26 ± 0.3 BCb
75	0.21 ± 0.05 Aa	3.69 ± 0.6 Cb	3.77 ± 0.2 Cb	5.22 ± 0.8 Cb

Means with the same upper case letter do not differ within water treatments (p>0.05).

Means with the same lower case letter do not differ within light treatments (p>0.05).

Table 5. *Microstegium vimineum* shoot biomass (g/plant; mean ± 1 standard error) at termination of light/water trade-off experiment

Light (%)	Target Volumetric Water Content (%)			
	10	20	30	40
2	0.03 ± 0.003 Aa	0.04 ± 0.005 ABa	0.03 ± 0.005 Aa	0.04 ± 0.007 Aa
5	0.17 ± 0.04 Aa	0.33 ± 0.03 BCab	0.43 ± 0.06 Ab	0.40 ± 0.07 Ab
10	1.00 ± 0.1 Ba	1.65 ± 0.2 CDa	1.67 ± 0.2 Ba	1.27 ± 0.4 Aa
25	1.34 ± 0.2 Ba	2.56 ± 0.4 DEb	2.64 ± 0.2 Cb	3.00 ± 0.3 Bb
75	0.20 ± 0.05 Aa	3.47 ± 0.6 Eb	3.50 ± 0.2 Db	4.69 ± 0.7 Cb

Means with the same upper case letter do not differ within water treatments (p>0.05).

Means with the same lower case letter do not differ within light treatments (p>0.05).

Table 6. *Microstegium vimineum* root biomass (g/plant; mean ± 1 standard error) at termination of light/water trade-off experiment

Light (%)	Target Volumetric Water Content (%)			
	10	20	30	40
2	0.008 ± 0 Aa	0.008 ± 0.0004 Aa	0.008 ± 0.0004 Aa	0.01 ± 0.002 Aa
5	0.008 ± 0 Aa	0.01 ± 0.001 Bb	0.06 ± 0.04 Bc	0.03 ± 0.02 Ab
10	0.09 ± 0.03 Ba	0.15 ± 0.02 Cb	0.46 ± 0.18 Cc	0.55 ± 0.27 Bc
25	0.06 ± 0.02 Ba	0.24 ± 0.09 Db	0.43 ± 0.1 Cc	0.26 ± 0.04 Bb
75	0.009 ± 0.0005 Ca	0.22 ± 0.08 Db	0.27 ± 0.05 Cb	0.54 ± 0.14 Bc

Means with the same upper case letter do not differ within water treatments (p>0.05).

Means with the same lower case letter do not differ within light treatments (p>0.05).

Table 7. *Microstegium vimineum* root:shoot ratios at termination of light/water trade-off experiment

Light (%)	Target Volumetric Water Content (%)			
	10	20	30	40
2	0.29 ± 0.03 Aa	0.26 ± 0.03 Aa	0.27 ± 0.03 Aa	0.42 ± 0.25 Aa
5	0.06 ± 0.01 Ba	0.04 ± 0.008 Ba	0.11 ± 0.06 Aa	0.06 ± 0.03 Aa
10	0.10 ± 0.04 Ba	0.09 ± 0.005 Ba	0.25 ± 0.09 Aa	0.39 ± 0.14 Aa
25	0.05 ± 0.01 Ba	0.10 ± 0.04 Ba	0.16 ± 0.03 Aa	0.09 ± 0.01 Aa
75	0.08 ± 0.03 Ba	0.07 ± 0.02 Ba	0.08 ± 0.02 Aa	0.12 ± 0.04 Aa

Means with the same upper case letter do not differ within water treatments (p>0.05).

Means with the same lower case letter do not differ within light treatments (p>0.05).

Table 8. Mean (± 1 standard error) emergence and biomass of 30-day-old *Microstegium vimineum* seedlings grown from soil collected beneath *Asimina triloba* in the Oak Ridge National Environmental Research Park, Oak Ridge, Tennessee, USA, in winter 2001/2002.

Experiment and Response Variable	Center		Intermediate		Inside Edge		Outside Edge	
	seeded	not seeded	seeded	not seeded	seeded	not seeded	seeded	not seeded
Pre-dispersal emergence (%)	80 ± 11 a	.0	86 ± 8 a	0	83 ± 7 a	0	86 ± 12 a	0
Pre-dispersal biomass (g/m^2)	5.0 ± 0.9 a	0	4.6 ± 0.6 a	0	6.8 ± 0.1 a	0	6.1 ± 1.3 a	0
Post-dispersal seedlings/m^2	NA	2 ± 1 a	NA	14 ± 6 a	NA	164 ± 73 a	NA	1706 ± 461 b

Means in the same row for seeded or not seeded treatments with the same letter did not differ (p>0.05).

Table 9. Growth response of *Microstegium vimineum* to experimental treatments within and outside of *Asimina triloba* patches in the Oak Ridge National Environmental Research Park, Oak Ridge, Tennessee, USA, in summer 2001

Contrast Number	Contrast Description	Treatment Codes	Survival		Height		Biomass	
			%	p-value	cm	p-value	g/m^2	p-value
1	Outside patch	5	96 ± 2	<0.0001	21 ± 1	0.003	2.3 ± 0.3	0.009
	Inside patch	1,2,3,4	43 ± 8		17 ± 1		1 ± 0.4	
2	Cut side	1,2	62 ±11	0.0005	17 ± 1	0.9	1.8 ± 0.7	0.001
	Uncut side	3,4	24 ± 9		17 ± 1		0.2 ± 0.1	
3	Cut side, not shaded	1	96 ± 2	<0.0001	18 ± 1	0.1	3.5 ± 0.9	<0.0001
	Cut side, shaded	2	26 ± 9		16 ± 1		0.04 ± 0.02	
4	Uncut side, not watered	3	28 ± 15	0.6	18 ± 2	0.1	0.22 ± 0.18	0.9
	Uncut side, watered	4	20 ± 11		15 ± 1		0.1 ± 0.09	
5	Outside patch	5	93 ± 2	0.8	21 ± 1	0.1	2.3 ± 0.3	0.07
	Inside patch, cut side, not shaded	1	96 ± 2		18 ± 1		3.5 ± 0.9	

Figure 1. Conceptual model of resource substitution with and without interaction. E represents the zero-growth isocline when resources A and B are perfectly substitutable (i.e., no interaction), and F represents the zero-growth isocline in the trade-off model. At any point along line E, plant performance is unaffected by a reduction of resource A by amount q_A as long as there is an equivalent increase in the availability of resource B by amount q_B. Conversely, an increase in resource B by amount q_B is inadequate compensation for a reduction in resource A by amount q_A , and plant performance falls from point C (above the zero growth isocline F) to point D (below the zero growth isocline F).

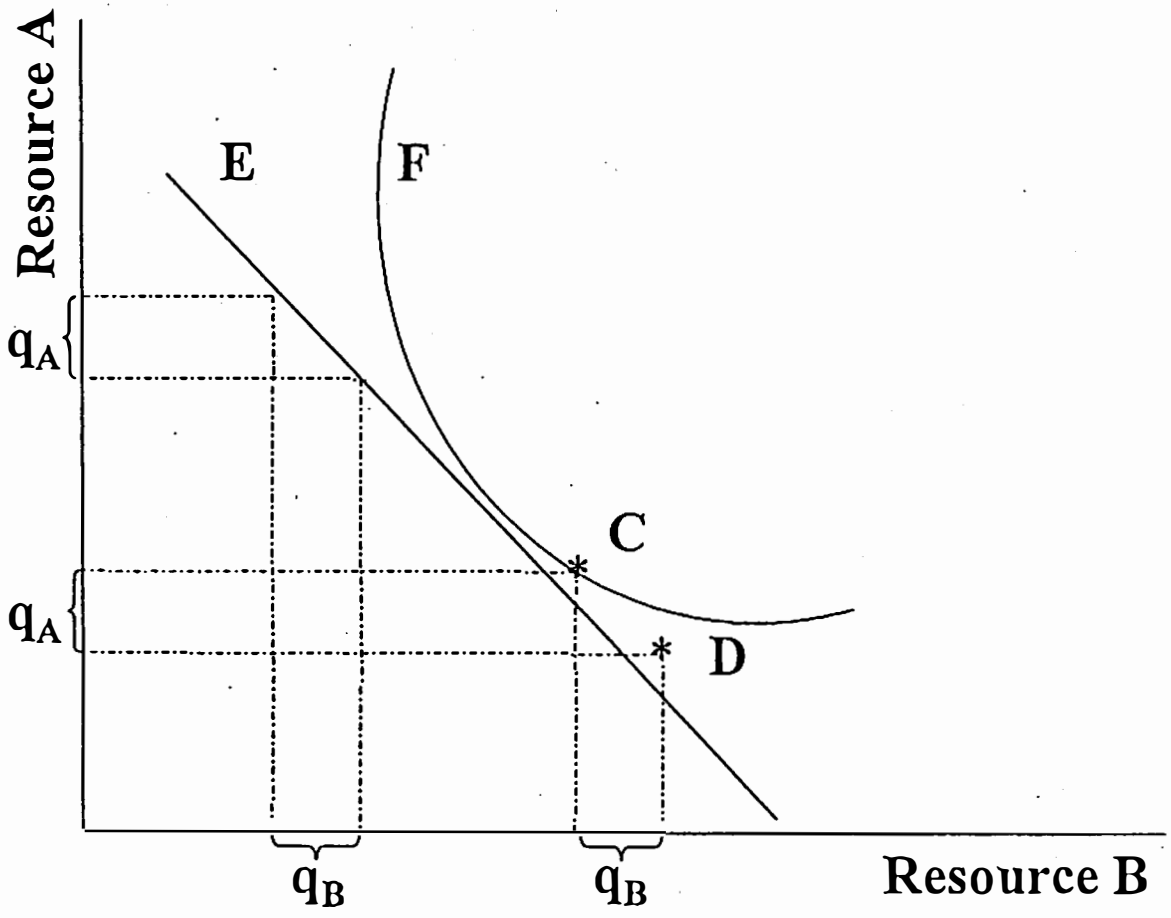

Figure 1. Conceptual Model of Resource Substitution With and Without Interaction

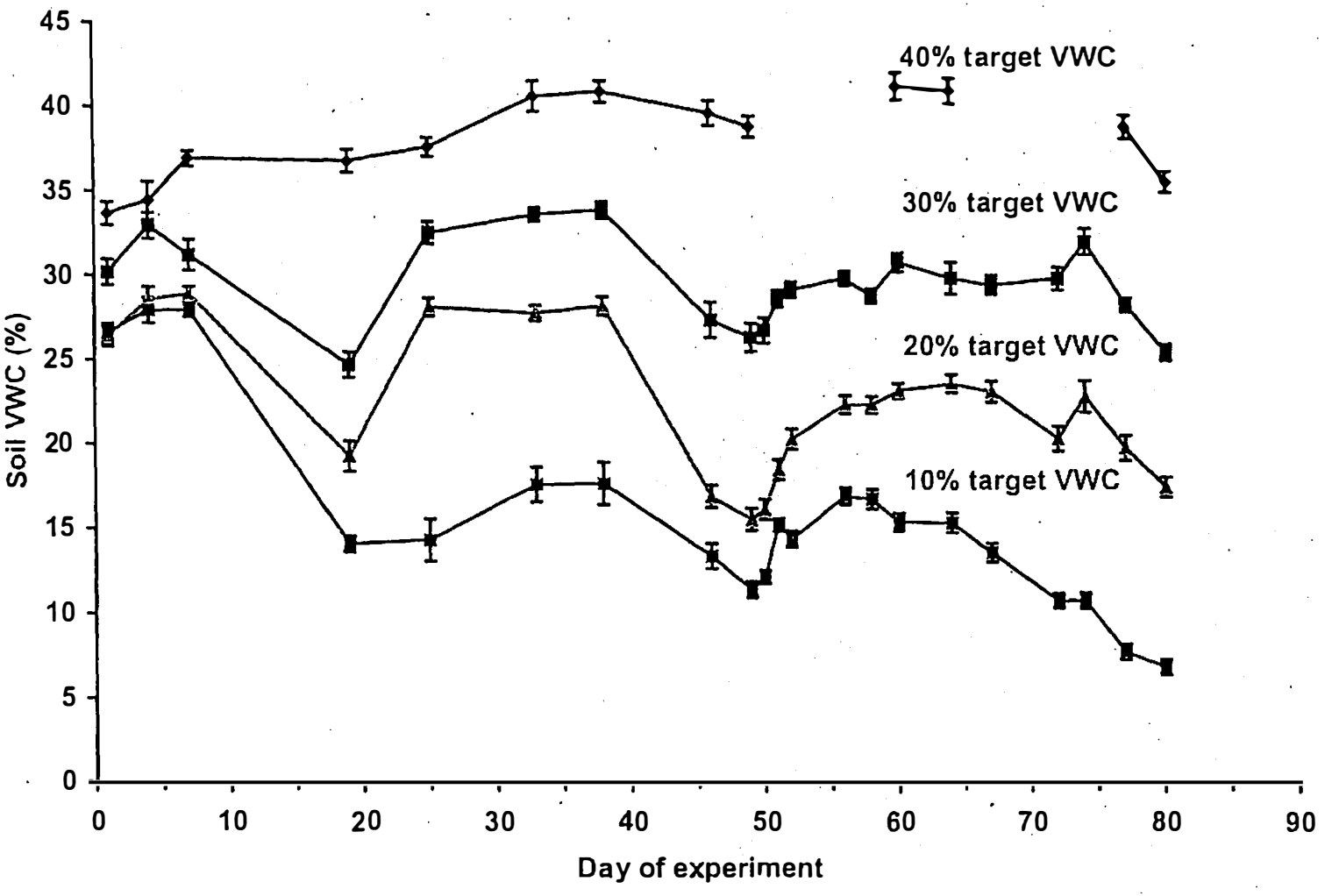

Figure 2. Soil Moisture Trends, *Microstegium vimineum* Light/Water Trade-off Experiment

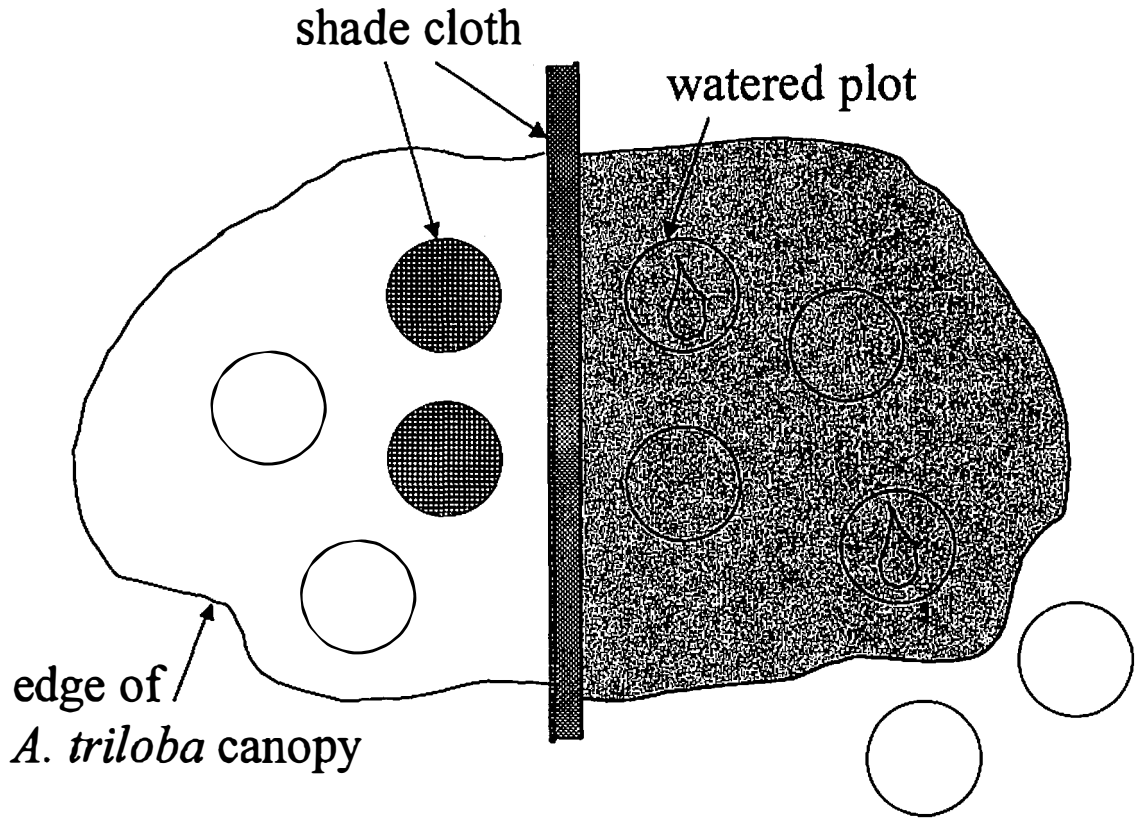

Figure 3. Schematic of experimental treatments within an *Asimina triloba* patch during an experiment conducted in the Oak Ridge National Environmental Research Park, summer 2001. *A. triloba* canopy was removed from the south side of the patch, and a shade cloth screen was suspended across the center of the patch. Experimental plots (0.25 m^2) were established within each half of the patch as well as outside the patch. Two plots in the cut side were covered with shade cloth, and two plots in the uncut side were watered weekly.

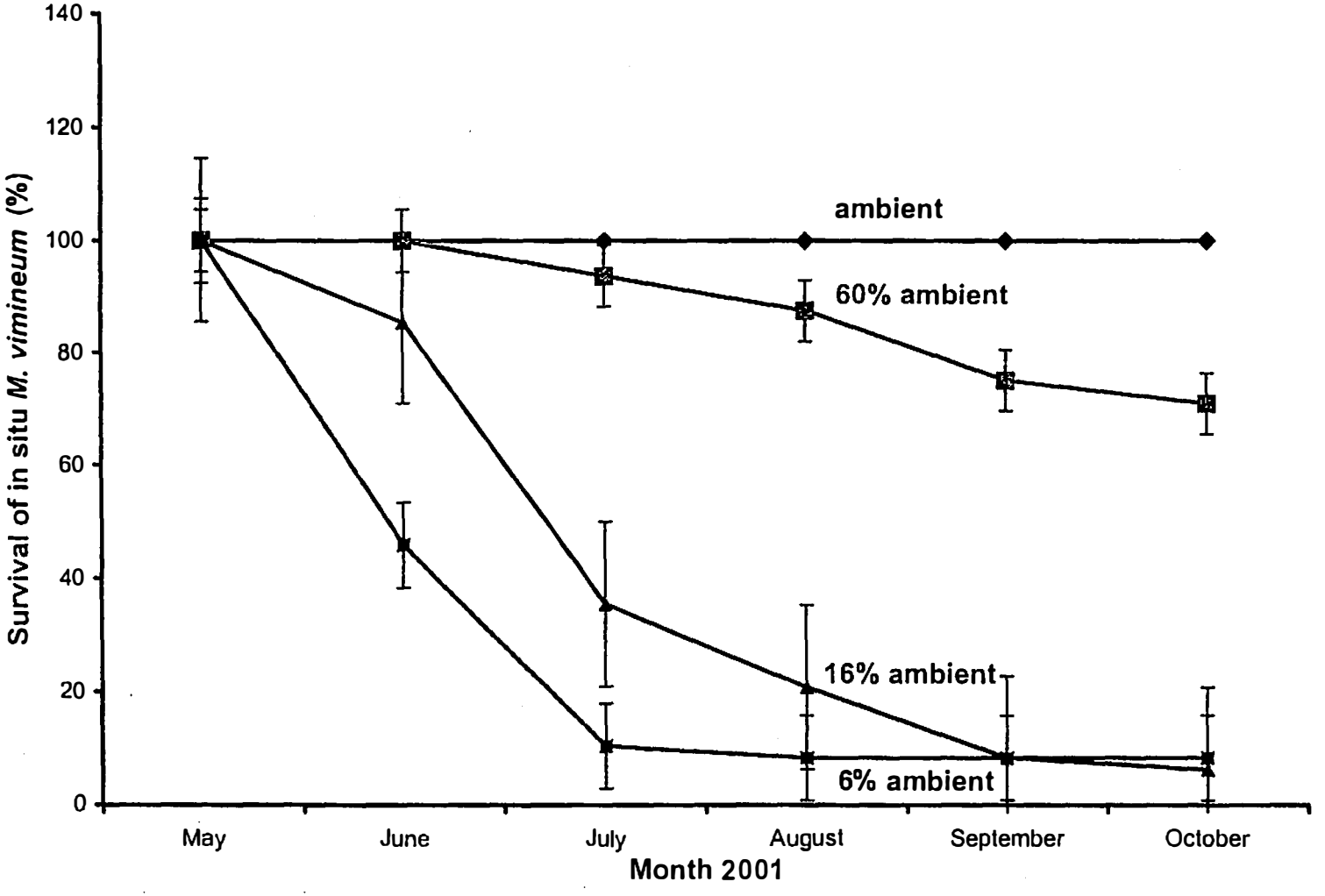

Figure 4. *Microstegium vimineum* Seedling Survival at Termination of Light Gradient Experiment

VITA

Patrice Gayle Cole received a Bachelor of Science degree in biology from Southeastern Louisiana University in 1975. She received a Master of Science in Planning degree, with a specialization in environmental planning, from the University of Tennessee in 1989. After a 20-year career in environmental regulatory compliance, including professional positions with industry, state regulatory agencies, and consulting firms, she earned a Doctor of Philosophy degree in ecology and evolutionary biology from the University of Tennessee in 2003. She is currently beginning a new career in teaching and research.